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INTERSPECIFIC HYBRIDIZATION IN LESQUERELLA[1]

REED C. ROLLINS AND OTTO T. SOLBRIG

The full ramification of interspecific hybridization as a mechanism for recombining the genetic materials of existing species, and the role this phenomenon may have played in the evolution of the present world biota is still without a complete and satisfactory formulation. This is true, in spite of the considerable research and the numerous publications on the subject. The research reported below contributes to an understanding of hybridization and its effects on populations.

Frequently, motivations for the study of wild hybrids have been associated with taxonomic problems that arise because of the complexity introduced by interspecific hybridization itself. However, in most of the auriculate species of *Lesquerella* such a problem does not exist. The wild hybrids participate in an existing situation that does not, at present, complicate the taxonomic picture of the species involved. The fact that populations of wild hybrids exist and are readily available for study, and that interspecific crosses can easily be made, makes certain of these species of *Lesquerella* desirable research material for examining the nature of species differences. We have been interested in various aspects of the genetic bases for the differences between species, and the way in which these differences are correlated with each other, both within and between species. The utilization of data from experimentally produced hybrids is an obvious way to approach these problems.

During the course of our study, we have again been impressed with the striking, dynamic changes that occur in populations of hybrids, especially in the Harpeth River valley. Some attention has been given to these aspects of the problem because of the general bearing they have on ways in which hybrids may participate in the recombination and dispersion of the genetic components of different species. We are aware of the possibility that entirely different taxa might arise and become stabilized at remote distances from the hybridizing parental species, a possibility suggested in a dramatic way by the Harpeth River valley populations. However, it should be emphasized that this has not occurred among the Lesquerellas of the area up to the present.

ACKNOWLEDGEMENTS

We have been assisted in the laboratory, greenhouse and experimental garden by Sharon Horn, Margaret Kunz, Mary Maly, Esperanza Vega and Roger Yocum, each of whom we thank very much for their committed efforts. We especially acknowledge the

[1]The first paper with this title, Interspecific Hybridization in Lesquerella (Cruciferae) by Reed C. Rollins was published in Contrib. Gray Herb. no. 181:1–40. 1957.

help given by Dr. William Bossert with computation and programming problems. We thank Dr. Warren H. Wagner for the use of facilities of the Botanical Gardens of the University of Michigan where the F_2 plants of the *Lesquerella densipila* × *L. lescurii* crosses were grown. Dr. James Farris permitted us to use his Prim program deck for the computation of linear similarity coefficients, which we very much appreciate.

Research supported by National Science Foundation grant GB-2019 to Reed C. Rollins, Principal Investigator.

OBJECTIVES

Rollins (1957) examined the extent and nature of interspecific hybridization among wild plants of the auriculate-leaved species of *Lesquerella* in Tennessee. It was established that there are virtually no genetical barriers between the four species of *Lesquerella* examined that were endemic to the Central Basin: *L. stonensis, L. perforata, L. lescurii* and *L. densipila*. Presumably these species arose in isolation from each other and have persisted allopatrically until recent times when, with man's help, three species have come together to produce interspecific hybrids. *Lesquerella densipila* and *L. lescurii* hybridize near the junction of Arrington Creek and the Harpeth River (Fig. 1). From that point down river for a distance of over 40 miles, there are numerous populations of hybrids on the flood plain of the Harpeth. *Lesquerella densipila* hybridizes with *L. stonensis* at the junction of the East Fork and the West Fork of Stones River (Fig. 1). From that point down river, only hybrid populations are to be found. In both these instances of interspecific hybridization, the hybrid populations occur downstream from the sites of the parental populations. This is because local migrations of the species are strongly affected by seasonal flooding of the streams of the Central Basin, the seeds being carried downstream. This unidirectional movement, particularly of the interspecific hybrids, is an important factor in maintaining the relative purity of the parental species populations. The tendency is for the species to move downstream until they come together, and for the resulting hybrids to continue to move downstream away from the areas where the parent species exist on the upper tributaries.

Such a situation is ideal to test several features of the hybrid populations and other aspects of the hybrids and parental species that are of more general interest. These include: (1) Is the variation of the hybrid populations greatest near the area where they are formed, or is it more or less uniform throughout? In other words, is natural selection favoring certain genotypes among the array present in the hybrid swarms in a way that the favored genotypes are more numerous farther downstream where presumably the influx of genes from the parental species is less intense? (2) What are the fluctuations exhibited by the hybrid swarms from year to year? That is, is the gene flow from both parental species uniform over time? (3) What is the inheritance mechanism of the characters by which these species are distinguished? (4) In these natural populations, do we encounter the phenomenon of "genetic coherence" (Clausen and Hiesey,

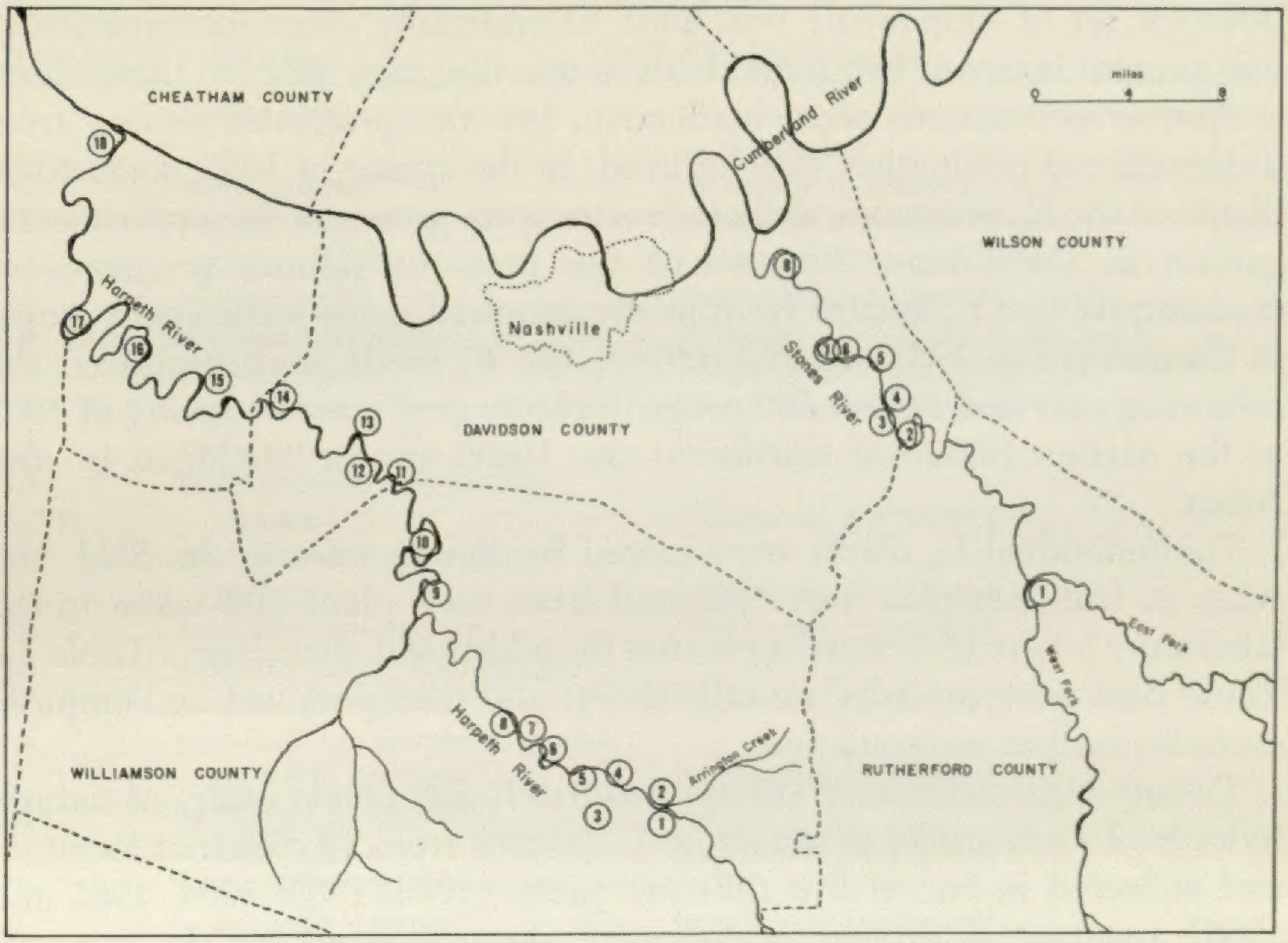

FIG. 1. Map of central Tennessee showing the collecting sites of *Lesquerella densipila* × *L. lescurii* hybrids along the Harpeth River and *L. densipila* × *L. stonensis* along the Stones River.

1960), a mechanism that favors the persistence of the parental genotypes in a greater frequency than would be expected if free recombination were operable?

Hybrids of the third combination, *Lesquerella lescurii* × *L. stonensis*, have only recently been discovered in LaVergne, Tennessee. These hybrids have not been studied in detail. The population is on a vacant lot in the town of LaVergne and is not associated with a stream system.

PROCEDURE AND METHODS

Progenies of wild populations (see Table 12 for localities of seed sources of five species of auriculate-leaved *Lesquerella–L. stonensis, L. perforata, L. lescurii, L. densipila, L. lyrata)* were grown in the greenhouses in Cambridge, Mass. during the winter and spring of 1961, and crossed in all 10 possible combinations. Nine of these were successful, the exception being the cross between *L. densipila* × *L. lescurii*. The following year F_1 progenies were grown in the greenhouse and sibling crosses performed. Since these species of *Lesquerella* are self-incompatible, no selfing was possible and sibling pollinations were required for viable seed set. There were some instances where cross incompatibility between individual

plants was present. When this was discovered in any particular pairing, a different set of individuals was used. Occasionally cross incompatibility was present between two individuals in one direction only. In these cases, reciprocal pollinations were ineffective, but the progenies arising from unidirectional pollination were utilized. In the spring of 1963, some 5,000 plants of the F_2 progenies of these crosses were grown in the experimental garden in Cambridge. Because of the previous failure, progenies of *L. densipila* and *L. lescurii* from newly acquired seeds were again grown in Cambridge in 1965 and hybridized; the F_2 seeds were produced the following year and some 1,500 progeny plants grown in the spring of 1967 at the Mathei Botanical Garden at the University of Michigan in Ann Arbor.

The individual F_2 plants were scored for flower color in the field, and when in fruit, samples were collected from each plant and taken to the laboratory where they were measured for additional characters (Table 1). These data were recorded on tally sheets and then punched on computer cards for further manipulations.

Twenty-eight accessions (of approximately 200 plants each) of natural hybrids of *Lesquerella densipila* × *L. lescurii* from 19 different localities and collected in one of five different years (1953, 1955, 1964, 1965 and 1966) spanning a 13 year period were also measured for the same 23 characters as the controlled hybrids and processed in the same way. Two sites are represented by four collections, three by two, and 14 by one. In addition, 12 samples of natural hybrids of *L. densipila* × *L. stonensis* were gathered and measured. These were from eight sites, and four collection years (1955, 1961, 1965 and 1966). Two sites were sampled in three different years, and six in only one. Finally, the following number of wild parental populations were sampled and measured in the same way as the artificial and wild hybrids: *L. densipila*, five populations over 13 years; *L. lescurii*, four populations over 13 years; *L. stonensis*, four populations over nine years; *L. lyrata*, two populations, both collected in 1955; and *L. perforata*, five populations over 11 years.

For every artificially produced F_2 progeny, as well as for every field sample, the mean, the standard deviation and the coefficient of variation of 23 characters was calculated. These are discussed in a subsequent section. In addition, simple correlation coefficients were calculated for every pair of characters for each F_2 progeny and each field sample. The results of these analyses can be found under the section Character Correlation. The calculations were performed on the IBM 7090 computer at Harvard University using programs written by one of us (OTS).

Finally, a linear similarity coefficient between populations was calculated according to the Prim diagram, using a program written by Dr. James Farris, and run on the IBM 7090 computer at the University of Michigan. The results of this analysis are discussed under the section on geographical and temporal variation of natural hybrids.

TABLE 1. CHARACTERS AND CHARACTER STATES

Character Number	*Character*	*Character States*
1	flower color	1=white; 2, 3, 4=graded intermediates; 5=yellow
2	style length	measured to nearest ¼ mm.
3	replum length	measured to nearest ¼ mm.
4	replum width	measured to nearest ¼ mm.
5	silique width	measured to nearest 0.1 mm.
6	septum perforation	0=none; 1=<½; 2=½; 3=>½
7	replum apex	0=rounded; 1=angular
8	replum base	0=rounded; 1=angular
9	trichomes at style base	0=absent; 1=present
10	trichomes on valve outer surface	0=absent; 1=present
11	trichomes on valve inner surface	0=absent; 1=present
12	trichomes on replum	0=absent; 1=present
13	bulbous simple trichomes on valve exterior	0=absent; 1=present
14	non-bulbous simple trichomes on valve exterior	0=absent; 1=present
15	branched non-stalked trichomes on valve exterior	0=absent; 1=present
16	branched stalked trichomes on valve exterior	0=absent; 1=present
17	type of trichomes on valve inner surface	0=none; 1=simple; 2=branched; 3=both simple and branched
18	silique apex	0=angular; 1=rounded; 2=depressed
19	length of pedicel	measured to nearest mm.
20	number of pedicels in 5 cm. of raceme	actual count
21	trichomes >0.48 mm. long on valve exterior	0=absent; 1=present
22	trichomes 0.16–0.48 mm. long on valve exterior	0=absent; 1=present
23	trichomes <0.16 mm. long on valve exterior	0=absent; 1=present

FIELD SETTING

The Central Basin of Tennessee is the residuum of a former giant limestone dome. Many of the resulting Ordovician limestone outcroppings form cedar glades throughout the basin. These glades are the favored sites of four sympatric species of *Leavenworthia* and they have been described in connection with studies of that genus (Rollins, 1963; Lloyd, 1965). The principal streams traversing this basin are the Stones and Harpeth rivers which arise in the eastern and south-central portions and flow northward into the Cumberland River. Cutting across the southern portion of the basin is the Duck River which flows almost directly west to join the Tennessee River. The Cumberland River transects the basin along its northern edge and flows westward for some distance past the limits of the basin before turning north.

The present distribution of the four auriculate-leaved species of *Les-*

querella in Tennessee is related to the streams, on the one hand, and to the cedar glades on the other. The distribution of each species is given in turn. The most restricted species is *L. perforata,* so far known only from the vicinity of Lebanon and a few miles to the north near Spring Creek, both localities in Wilson County. However, the presently known distribution may reflect, in part at least, the fact that no concerted effort has been made to extend the range by carefully searching for other occurrences of this species, especially downstream from the Spring Creek locality. *Lesquerella perforata* is on disturbed land in a glade area near Lebanon, but it is possible this is a recent invasion from elsewhere. It is not certain that this taxon is naturally in a glade situation but the population on Spring Creek confirms that it is at least associated with a stream in one area of its occurrence.

Lesquerella stonensis is mostly associated with the East Fork of Stones River, occurring on the flood plain and adjacent areas, but it is also known from one location about one and one-half miles east of the river in an uncultivated cedar glade-like area. The species proper, unadulterated from hybridization, is at present known only from within Rutherford County.

The most widespread species of the group is *Lesquerella densipila* but the present distribution appears to be somewhat more extensive than its pristine range. In the Central Basin it is abundant in the area of the upper Harpeth River, along the Duck River and on the upper portion of the West Fork of Stones River. There are many sites that are essentially cedar glades even though they are somewhat modified from the original by pasturage or other land use. *Lesquerella densipila* also occurs in southern Tennessee and in northern Alabama. Since our first observations of it in 1952, this species appears to have increased its geographic area, perhaps being carried about in hay or by farm machinery.

Lesquerella lescurii is common in the northern portion of the Central Basin, especially in the area of Nashville, where it is found most commonly on cedar glade sites. However, it has spread along the Cumberland River bottom up to the "rim" of the basin at some distance northwest of Nashville and is found on several tributaries of the Harpeth River. There is evidence that *L. lescurii* is actively expanding its range at the present time both by natural means and through man's activities.

It is clear that, basically the above four species of *Lesquerella* are allopatric in their distributions. Each appears to have evolved in relationship to one of the streams of the Central Basin, perhaps not in the stream valley itself but more likely in the glade-like areas exposed by the erosion of the land surface by small tributaries arising on high ground. *Lesquerella perforata* is associated with Spring Creek, *L. stonensis* with the Stones River, *L. densipila* with the Duck River and *L. lescurii* with the Cumberland River. The fact that three of the four species have now come together, and produced interspecific hybrids does not, in our judgment, negate the

basic pattern of allopatry. Rather, this is explainable on the basis that the ranges of the species have become altered in recent years, most probably through intensive agricultural activities in the area.

Lesquerella lyrata is restricted to a few known sites in the glade region of northern Alabama. The only other *Lesquerella* in Alabama is *L. densipila,* somewhat to the east of the range of *L. lyrata.* We believe *L. densipila* is probably a recent introduction into Alabama from Tennessee. In any case, the ranges of *L. lyrata* and *L. densipila* do not overlap.

DESCRIPTION OF THE CHARACTERS

Because of the convenience and ease of sampling and because the vegetative parts of all five species are quite similar, a large proportion of the characters measured or scored were those concerned with the siliques and infructescences. But there are other reasons for concentrating on fruit characters, as here many of the specific differences can be seen. Developmentally, the siliques reach a state of maturity quite rapidly and then remain the same for a relatively long period. Thus, problems of size changes associated with development were avoided by always sampling the oldest fully mature siliques. In this way, a comparability of samples was achieved that would be difficult to accomplish otherwise. The characters and the coding indicators are given in Table 1. However, some further comments on several of the characters are required for clarity.

Flower color. The two basic patterns are all yellow with darker guidelines in the center of the flower and all white except for the yellow center in which the guidelines are the deepest yellow. The coloring of the yellow-flowered species, *Lesquerella lescurii, L. lyrata* and *L. densipila,* is similar with only minor variations in the intensity of the yellow. The most intense color is in the center of the flower and this tends toward orange. White flowers are characteristic of *L. perforata* and *L. stonensis.* Crosses between species of the same flower color result in progeny with the same color in both F_1 and F_2. However, crosses between yellow- and white-flowered species produce an intermediate flower color in the first generation and then segregated forms ranging from nearly white to nearly pure yellow among the F_2 individuals. In scoring these hybrids and those from field populations, we used 1 and 5 for the white and yellow respectively, 3 for the median intermediate, 2 for individuals tending toward white from the median and 4 for those tending toward yellow from the median.

Style length. In *Lesquerella* as a whole, the length of the style differs considerably from species to species. However, among the auriculate-leaved species this is not the case. Measurements were taken mainly to test whether this easily taken statistic could be utilized in any definite way.

Replum length. The replum, which can be readily exposed by taking off one of the valves, is easily measured. The length is also a measure of the silique length and important in showing the overall shape of the silique.

Replum width. This second dimension of the replum provides the basis for knowing the thickness of the silique as well as the shape of the replum itself.

Silique width. Of the species under consideration, *Lesquerella lescurii* with its flattened siliques is at one extreme and *L. stonensis*, with somewhat distended valves is at the other. This dimension discriminates *L. lescurii* from the other species which have fruits nearly alike.

Septum perforation. In most species of *Lesquerella* the septum is without any perforation. When a perforation is present (Fig. 2B) and of small size, it is usually at or near the center of the septum. The most extreme case of septum perforation is that of *L. perforata*, where nearly the entire septum is missing (Fig. 2C). This feature is less pronounced in *L. stonensis* but there is usually a hole present in the septum of this species. The other species of the group usually have imperforate septa.

Replum apex and base. The angle at which the replum apex meets the base of the style varies from rounded, as in *L. densipila*, to angular, as in *L. lescurii*. This is true also at the base of the replum where it joins the receptacle. These two features (Fig. 2A, B) were scored separately for the apex and base of the replum.

Trichomes: presence, absence and type. A number of variations in the types of trichomes and in their presence or absence occur among the auriculate species of *Lesquerella* in such a way as to offer discriminating

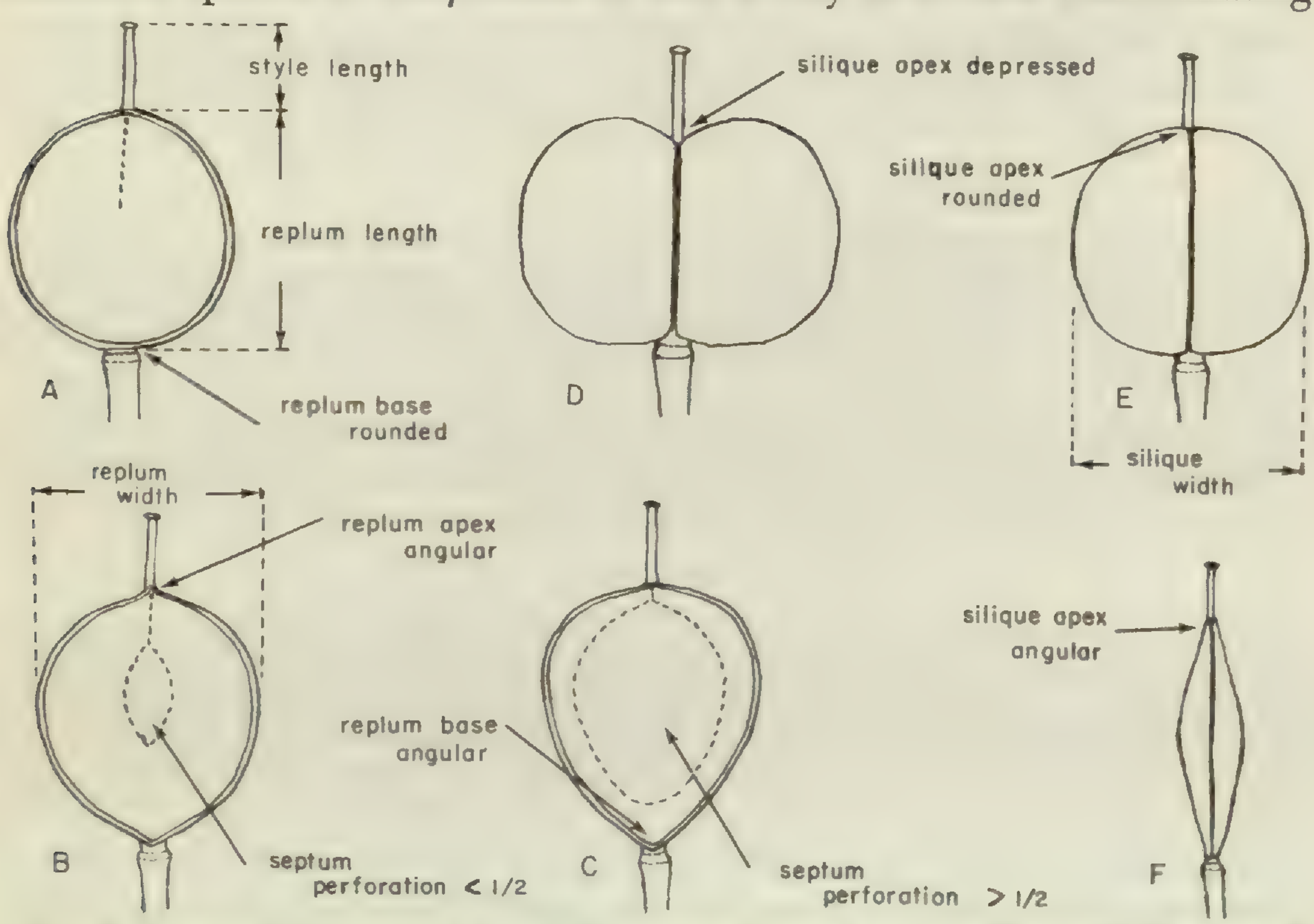

FIG. 2. Sketches of *Lesquerella* siliques. A. Replum without a septum perforation and with an indication of style length and replum length measurement limitations. B. Replum showing septum perforation of less than one-half and an indication of replum width measurement limitations. C. Replum showing septum perforation greater than one-half. D. Silique showing depressed apex. E. Silique showing rounded apex and measurement limits for silique width. F. Silique showing angular apex.

combinations. The extreme example of the lack of trichomes on the silique is *L. lyrata* where all parts are completely glabrous. The siliques of *L. densipila* are densely covered with simple trichomes while those of *L. lescurii* have two types of trichomes on the exterior as well as branched trichomes on the interior. In each of the character states separately scored, at least one species of the group features the alternative state. For example, trichomes are not at the style base in *L. lescurii*, whereas they are nearly always present in *L. densipila* and *L. stonensis*. Similarly, trichomes are always present on the interior of the valves in *L. perforata* but they are absent in *L. stonensis*. Of the simple trichomes found among the five species, the most extreme are the large, almost acicular bulbous-based type found in *L. lescurii* and the minute unthickened ones found in *L. densipila*. Branched trichomes are present on the valve surfaces of *L. lescurii* and on the interior of the valves of *L. perforata*.

Silique apex. Whether the silique apex is angular (that is, more or less acute), rounded, or depressed (Fig. 2D, E, F) when viewed from the replum margin was recorded. *Lesquerella lescurii* has angular siliques while those of *L. densipila* and *L. lyrata* are rounded. Some siliques of *L. perforata* and nearly all of *L. stonensis* are depressed.

Other characters. The last five characters listed in the tables are designed to show up differences in length of pedicels and trichomes and to give a measure of the density of fruits in the infructescences. The trichomes measured were those on the silique surface.

Artificial Hybrids

First we will briefly describe the salient features of the artificial crosses. Since the analysis comprises a total of 5,400 plants, including 1,530 parental species individuals, 3,170 F_2 and 600 backcross progeny in 71 different genetical families (23 parental, 60 F_2 and 8 backcross) only a summary emphasizing the relevant aspects can be presented here.[2]

Tables 2 to 11 list the range and mean for the 23 characters measured for each of the crosses. The comparison is between one particular artificial F_2 hybrid population grown in the garden and the sum of all populations from the wild of the parental species. Because the F_2 and the parents grew in different environments, a definite environmental effect is to be expected.

An inspection of Tables 2 to 11 reveals that not all species differ in all 23 characters. When they do differ in a character, the hybrid may show a value intermediate between that of the parents, equal to that of one parent but not the other, or it may transcend the values exhibited by either parent. Out of a total of 230 individual pair-by-pair comparisons (23 characters in 10 crosses), 40 pairs show similar values for parents and

[2]The score sheets and detailed analysis have been filed in the library of the Gray Herbarium together with this report and are available for scrutiny by interested individuals.

hybrids. Of the remaining 190, 96 (about 50%) show values that are intermediate between those of the parents, 25% have values that closely approximate one parent, and 25% have values transcending both parents. Certain characters, such as shape of the replum apex and base or length of pedicel, have a greater tendency to deviate from the expected intermediacy. Most of these are size characters. Since these are characters showing the greatest response to the cultural conditions, most, if not all, of the apparent dominance has to be attributed to luxuriance and not to genetic overdominance. Further inspection also reveals that the greater the magnitude of the difference in the two parental values, the greater the probability that the hybrid will be intermediate. If the environmental effect is fixed in its magnitude rather than proportional to the difference, the above observation is expected. Consequently, it can be assumed that the hybrids are intermediate in most, if not all, their characters.

The lack of data on the actual parents and F_1 hybrids precludes drawing any conclusions regarding the genetic mechanism that controls the characters measured, other than the obvious one that none is controlled by a simple, 1- or 2-locus system. However, it is probable they are all inherited in a multigenic fashion, including the pubescence characters.

Lesquerella densipila × L. lescurii—Field Populations

The series of hybrid swarms produced by these species are by far the most interesting because of their extension over a distance of more than 70

Table 2. Data from L. perforata, L. stonensis and their F_2 progenies

	perforata N=181			*perforata* × *stonensis* N=212			*stonensis* N=216		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
style length	2.00	2.50	2.21	1.80	2.53	2.24	2.16	2.44	2.26
replum length	3.75	4.79	4.19	3.88	4.59	4.08	3.60	4.33	3.95
replum width	3.85	5.00	4.32	3.50	3.94	3.82	3.54	3.99	3.71
silique width	4.34	5.43	4.78	3.88	4.74	4.54	4.09	4.91	4.44
septum perfor.	3.00	3.07	3.01	2.31	2.89	2.60	1.48	1.73	1.59
replum apex	0.07	0.75	0.51	0.44	0.91	0.69	0.40	0.72	0.57
replum base	0.00	0.55	0.23	0.23	0.67	0.29	0.02	0.15	0.07
trich.: style-base	0.00	0.02	0.01	0.44	0.73	0.56	0.90	1.00	0.97
trich.: out. valve	0.64	0.93	0.73	0.77	1.00	0.88	1.00	1.00	1.00
trich.: inn. valve	1.00	1.00	1.00	0.71	0.84	0.74	0.00	0.00	0.00
trich.: replum	0.00	0.59	0.31	0.72	0.92	0.78	1.00	1.00	1.00
trich.: bulbous	0.00	0.21	0.06	0.00	0.00	0.00	0.00	0.00	0.00
trich.: nonbulb.	0.12	0.50	0.33	0.63	0.84	0.74	1.00	1.00	1.00
trich.: nonstalk.	0.29	0.68	0.36	0.44	0.89	0.69	0.00	0.00	0.00
trich.: stalked	0.30	0.71	0.48	0.66	0.79	0.73	0.00	0.03	0.01
trich. type: inn.	2.00	2.00	2.00	1.67	2.22	1.81	0.00	0.00	0.00
silique apex	1.89	2.00	1.93	1.32	1.96	1.68	1.44	1.72	1.59
pedicel length	0.74	1.03	0.93	1.02	1.25	1.14	0.82	1.35	1.06
pedicel no.	1.11	1.67	1.38	1.21	1.54	1.33	0.06	1.21	0.76
trich.>.48 mm.	0.11	0.43	0.18	0.00	0.31	0.14	0.00	0.02	0.01
trich. .16–.48 mm.	0.42	0.71	0.55	0.53	0.90	0.77	0.98	1.00	1.00
trich.<.16	0.17	0.68	0.34	0.77	1.00	0.84	0.98	1.00	1.00

miles, from the junction of the upper Harpeth River and Arrington Creek in Williamson County to the junction of the Harpeth with the Cumberland River in Cheatham County. We have sampled a total of 18 localities over this area and over a period of 13 years (Fig. 1 and Table 13).

The hybrid swarms are usually found in alluvial flood plains on the upper side of long bends of the river. These areas are sometimes covered with the natural vegetation of such areas; in other cases they are pastures or are regularly cultivated. Our observations indicate that the populations are capable of maintaining themselves at least over a period of years. However, they show marked changes in numbers and occasionally also in resemblance to one or the other parent species, indicating that new seed is arriving at the sites from places upstream, and that the populations can be wiped out by unfavorable conditions. A good example is the population at the junction of Arrington Creek and the Harpeth River (Site 1). In 1955 this population was estimated by one of us (Rollins, 1957) to occupy an area of approximately 600 acres, and the plants to be intermediate in their characteristics to the two parental species. By 1964, the population area had been reduced considerably and the plants now resembled *Lesquerella densipila* more than *L. lescurii*. In 1966, an extensive search resulted in a find of less than 10 plants. The area by then had been converted into pasture land. Whether this observation is representative on how transient these populations really are is hard to ascertain. What we

TABLE 3. DATA FROM L. PERFORATA, L. LYRATA AND THEIR F_2 PROGENIES

	perforata N=181			*perforata* × *lyrata* N=608			*lyrata* N=130		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	1.00	1.00	1.00	1.95	2.54	2.19	5.00	5.00	5.00
style length	2.00	2.50	2.21	1.79	2.29	2.00	1.71	1.84	1.77
replum length	3.75	4.79	4.19	4.40	5.02	4.69	3.22	3.38	3.30
replum width	3.85	5.00	4.32	3.57	4.40	3.94	3.29	3.46	3.37
silique width	4.34	5.43	4.78	4.49	4.98	4.80	3.62	3.65	3.63
septum perfor.	3.00	3.07	3.01	1.42	1.94	1.74	0.00	0.03	0.02
replum apex	0.07	0.75	0.51	0.63	0.75	0.71	0.00	0.02	0.01
replum base	0.00	0.55	0.23	0.31	0.71	0.52	0.00	0.00	0.00
trich.: style-base	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00
trich.: out. valve	0.64	0.93	0.73	0.02	0.13	0.04	0.00	0.07	0.03
trich.: inn. valve	1.00	1.00	1.00	0.59	0.73	0.67	0.00	0.00	0.00
trich.: replum	0.00	0.59	0.31	0.00	0.01	0.00	0.00	0.07	0.03
trich.: bulbous	0.00	0.21	0.06	0.00	0.01	0.00	0.00	0.00	0.00
trich.: nonbulb.	0.12	0.50	0.33	0.00	0.01	0.00	0.00	0.07	0.03
trich.: nonstalk.	0.29	0.68	0.36	0.00	0.08	0.03	0.00	0.00	0.00
trich.: stalked	0.30	0.71	0.48	0.00	0.11	0.02	0.00	0.00	0.00
trich. type: inn.	2.00	2.00	2.00	1.20	1.50	1.36	0.00	0.00	0.00
silique apex	1.89	2.00	1.93	1.21	1.62	1.33	1.82	1.83	1.82
pedicel length	0.74	1.03	0.93	1.12	1.26	1.19	0.88	1.00	0.94
pedicel no.	1.11	1.67	1.38	1.46	1.71	1.60	1.11	1.50	1.32
trich.>.48 mm.	0.11	0.43	0.18	0.00	0.01	0.00	0.00	0.00	0.00
trich. .16–.48 mm.	0.42	0.71	0.55	0.00	0.11	0.03	0.00	0.00	0.00
trich.<.16	0.17	0.68	0.34	0.00	0.30	0.02	0.00	0.07	0.03

TABLE 4. DATA FROM L. PERFORATA, L. LESCURII AND THEIR F_2 PROGENIES

	perforata N=181			*perforata* × *lescurii* N=84			*lescurii* N=324		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	1.00	1.00	1.00	1.78	2.27	2.03	5.00	5.00	5.00
style length	2.00	2.50	2.21	1.88	2.28	2.08	1.43	1.74	1.57
replum length	3.75	4.79	4.19	4.98	5.63	5.31	4.50	5.04	4.68
replum width	3.85	5.00	4.32	4.06	4.30	4.18	3.36	3.88	3.75
silique width	4.34	5.43	4.78	3.30	3.72	3.50	1.51	2.01	1.68
septum perfor.	3.00	3.07	3.01	1.38	1.62	1.50	0.01	0.08	0.03
replum apex	0.07	0.75	0.51	0.71	0.67	0.69	0.61	0.93	0.67
replum base	0.00	0.55	0.23	0.12	0.32	0.21	0.00	0.77	0.29
trich.: style-base	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00
trich.: out. valve	0.64	0.93	0.73	0.88	0.98	0.93	1.00	1.00	1.00
trich.: inn. valve	1.00	1.00	1.00	0.98	1.00	0.99	0.86	1.00	0.95
trich.: replum	0.00	0.59	0.31	0.00	0.00	0.00	0.00	0.05	0.01
trich.: bulbous	0.00	0.21	0.06	0.59	0.72	0.65	1.00	1.00	1.00
trich.: nonbulb.	0.12	0.50	0.33	0.51	0.19	0.35	0.00	0.11	0.03
trich.: nonstalk.	0.29	0.68	0.36	0.85	0.88	0.87	0.41	1.00	0.90
trich.: stalked	0.30	0.71	0.48	0.81	0.85	0.83	0.12	0.84	0.71
trich. type: inn.	2.00	2.00	2.00	1.93	1.98	1.95	1.76	2.00	1.92
silique apex	1.89	2.00	1.93	0.05	0.22	0.13	0.00	0.00	0.00
pedicel length	0.74	1.03	0.93	1.02	1.15	1.09	0.87	1.05	0.94
pedicel no.	1.11	1.67	1.38	1.33	1.52	1.43	1.11	1.68	1.33
trich.>.48 mm.	0.11	0.43	0.18	0.63	0.77	0.70	1.00	1.00	1.00
trich. .16–.48 mm.	0.42	0.71	0.55	0.72	0.83	0.77	0.07	1.00	0.81
trich.<.16	0.17	0.68	0.34	0.37	0.51	0.44	0.41	1.00	0.90

TABLE 5. DATA FROM L. PERFORATA, L. DENSIPILA AND THEIR F_2 PROGENIES

	perforata N=181			*perforata* × *densipila* N=43			*densipila* N=678		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	1.00	1.00	1.00			2.28	5.00	5.00	5.00
style length	2.00	2.50	2.21			2.23	1.59	1.92	1.73
replum length	3.75	4.79	4.19			4.76	3.06	3.61	3.37
replum width	3.85	5.00	4.32			3.59	3.11	3.53	3.19
slique width	4.34	5.43	4.78			4.25	3.03	3.90	3.51
septum perfor.	3.00	3.07	3.01			1.21	0.00	0.07	0.02
replum apex	0.07	0.75	0.51			0.77	0.00	0.63	0.27
replum base	0.00	0.55	0.23			0.47	0.00	0.62	0.24
trich.: style-base	0.00	0.02	0.01			0.72	0.12	1.00	0.73
trich.: out. valve	0.64	0.93	0.73			0.84	1.00	1.00	1.00
trich.: inn. valve	1.00	1.00	1.00			0.81	0.00	0.04	0.01
trich.: replum	0.00	0.59	0.31			0.74	0.97	1.00	0.99
trich.: bulbous	0.00	0.21	0.06			0.00	0.00	0.00	0.00
trich.: nonbulb.	0.12	0.50	0.33			0.35	1.00	1.00	1.00
trich.: nonstalk.	0.29	0.68	0.36			0.81	0.00	0.95	0.31
trich.: stalked	0.30	0.71	0.48			0.58	0.00	0.54	0.16
trich. type: inn.	2.00	2.00	2.00			1.79	0.00	0.11	0.03
silique apex	1.89	2.00	1.93			1.30	0.98	1.72	1.19
pedicel length	0.74	1.03	0.93			1.06	0.79	1.18	0.95
pedicel no.	1.11	1.67	1.38			1.62	1.31	1.58	1.49
trich.>.48 mm.	0.11	0.43	0.18			0.02	0.00	0.01	0.00
trich. .16–.48 mm.	0.42	0.71	0.55			0.56	0.00	0.30	0.08
trich. <.16	0.17	0.68	0.34			0.84	1.00	1.00	1.00

TABLE 6. DATA FROM L. STONENSIS, L. LYRATA AND THEIR F_2 PROGENIES

	stonensis N=216			*stonensis* × *lyrata* N=36			*lyrata* N=130		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	1.00	1.00	1.00	0.00	2.42	1.97	5.00	5.00	5.00
style length	2.16	2.44	2.26	1.76	2.00	1.85	1.71	1.84	1.77
replum length	3.60	4.33	3.95	4.00	4.91	4.72	3.22	3.38	3.30
replum width	3.54	3.99	3.71	2.83	3.34	3.19	3.29	3.46	3.37
silique width	4.09	4.91	4.44	3.96	4.22	4.06	3.62	3.65	3.63
septum perfor.	1.48	1.73	1.59	0.27	0.83	0.44	0.00	0.03	0.02
replum apex	0.40	0.72	0.57	0.27	0.67	0.53	0.00	0.02	0.01
replum base	0.02	0.15	0.07	0.11	0.46	0.22	0.00	0.00	0.00
trich.: style-base	0.90	1.00	0.97	0.00	0.16	0.08	0.00	0.00	0.00
trich.: out. valve	1.00	1.00	1.00	0.36	0.67	0.56	0.00	0.07	0.03
trich.: inn. valve	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
trich.: replum	1.00	1.00	1.00	0.36	0.67	0.53	0.00	0.07	0.03
trich.: bulbous	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
trich.: nonbulb.	1.00	1.00	1.00	0.27	0.37	0.33	0.00	0.07	0.03
trich.: nonstalk.	0.00	0.00	0.00	0.36	0.67	0.53	0.00	0.00	0.00
trich.: stalked	0.00	0.03	0.01	0.36	0.50	0.44	0.00	0.00	0.00
trich. type: inn.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
silique apex	1.44	1.72	1.59	0.91	1.17	0.97	1.82	1.83	1.82
pedicel length	0.82	1.35	1.06	0.83	0.94	0.91	0.88	1.00	0.94
pedicel no.	0.06	1.21	0.76	1.12	1.62	1.38	1.11	1.50	1.32
trich.>.48 mm.	0.00	0.02	0.01	0.09	0.11	0.08	0.00	0.00	0.00
trich. .16–.48 mm.	0.98	1.00	1.00	0.36	0.50	0.42	0.00	0.00	0.00
trich.<.16	0.98	1.00	1.00	0.36	0.67	0.50	0.00	0.07	0.03

TABLE 7. DATA FROM L. STONENSIS, L. LESCURII AND THEIR F_2 PROGENIES

	stonensis N=216			*stonensis* × *lescurii* N=443			*lescurii* N=324		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	1.00	1.00	1.00	2.49	2.94	2.62	5.00	5.00	5.00
style length	2.16	2.44	2.26	1.86	2.46	2.14	1.43	1.74	1.57
replum length	3.60	4.33	3.95	5.17	5.94	5.66	4.50	5.04	4.68
replum width	3.54	3.99	3.71	4.06	4.31	4.24	3.36	3.88	3.75
silique width	4.09	4.91	4.44	2.99	3.29	3.13	1.51	2.01	1.68
septum perfor.	1.48	1.73	1.59	0.60	1.26	0.60	0.01	0.08	0.03
replum apex	0.40	0.72	0.57	0.39	0.86	0.59	0.61	0.93	0.67
replum base	0.02	0.15	0.07	0.06	0.22	0.13	0.00	0.77	0.29
trich.: style-base	0.90	1.00	0.97	0.08	0.22	0.11	0.00	0.00	0.00
trich.: out. valve	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
trich.: inn. valve	0.00	0.00	0.00	0.26	0.77	0.57	0.86	1.00	0.95
trich.: replum	1.00	1.00	1.00	0.43	0.72	0.59	0.00	0.05	0.01
trich.: bulbous	0.00	0.00	0.00	0.50	0.79	0.64	1.00	1.00	1.00
trich.: nonbulb.	1.00	1.00	1.00	0.44	0.66	0.59	0.00	0.11	0.03
trich.: nonstalk.	0.00	0.00	0.00	0.64	0.91	0.82	0.41	1.00	0.90
trich.: stalked	0.00	0.03	0.01	0.61	0.94	0.79	0.12	0.84	0.71
trich. type: inn.	0.00	0.00	0.00	0.57	1.66	1.20	1.76	2.00	1.92
silique apex	1.44	1.72	1.59	0.00	0.22	0.09	0.00	0.00	0.00
pedicel length	0.82	1.35	1.06	0.97	1.31	1.14	0.87	1.05	0.94
pedicel no.	0.06	1.21	0.76	1.09	1.79	1.37	1.11	1.68	1.33
trich.>.48 mm.	0.00	0.02	0.01	0.52	0.94	0.77	1.00	1.00	1.00
trich. .16–.48 mm.	0.98	1.00	1.00	0.96	1.00	0.98	0.07	1.00	0.81
trich.<.16	0.98	1.00	1.00	0.73	1.00	0.94	0.41	1.00	0.90

TABLE 8. DATA FROM L. STONENSIS, L. DENSIPILA AND THEIR F_2 PROGENIES

	stonensis N=216			*stonensis* × *densipila* N=312			*densipila* N=678		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	1.00	1.00	1.00	2.30	3.61	3.11	5.00	5.00	5.00
style length	2.16	2.44	2.26	1.87	2.20	2.07	1.59	1.92	1.73
replum length	3.60	4.33	3.95	3.53	3.89	3.72	3.06	3.61	3.37
replum width	3.54	3.99	3.71	2.97	3.31	3.21	3.11	3.53	3.19
silique width	4.09	4.91	4.44	3.63	4.25	3.91	3.03	3.90	3.51
septum perfor.	1.48	1.73	1.59	0.01	0.20	0.08	0.00	0.07	0.02
replum apex	0.40	0.72	0.57	0.10	0.42	0.23	0.00	0.63	0.27
replum base	0.02	0.15	0.07	0.17	0.71	0.42	0.00	0.62	0.24
trich.: style-base	0.90	1.00	0.97	0.84	1.00	0.94	0.12	1.00	0.73
trich.: out. valve	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
trich.: inn. valve	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.01
trich.: replum	1.00	1.00	1.00	0.90	1.00	1.00	0.97	1.00	0.99
trich.: bulbous	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
trich.: nonbulb.	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
trich.: nonstalk.	0.00	0.00	0.00	0.47	0.77	0.66	0.00	0.95	0.31
trich.: stalked	0.00	0.03	0.01	0.02	0.70	0.18	0.00	0.54	0.16
trich. type: inn.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.03
silique apex	1.44	1.72	1.59	1.09	1.13	1.04	0.98	1.72	1.19
pedicel length	0.82	1.35	1.06	0.79	1.01	0.91	0.79	1.18	0.95
pedicel no.	0.06	1.21	0.76	1.37	1.85	1.61	1.31	1.58	1.49
trich.>.48 mm.	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.01	0.00
trich. .16–.48 mm.	0.98	1.00	1.00	0.23	0.70	0.38	0.00	0.30	0.08
trich.<.16	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

TABLE 9. DATA FROM L. LYRATA, L. LESCURII AND THEIR F_2 PROGENIES

	lyrata N=130			*lyrata* × *lescurii* N=273			*lescurii* N=324		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00
style length	1.71	1.84	1.77	1.44	1.94	1.89	1.43	1.74	1.57
replum length	3.22	3.38	3.30	4.63	4.80	4.70	4.50	5.04	4.68
replum width	3.29	3.46	3.37	3.68	4.14	4.03	3.36	3.88	3.75
silique width	3.62	3.65	3.63	2.72	2.86	2.76	1.51	2.01	1.68
septum perfor.	0.00	0.03	0.02	0.00	0.02	0.01	0.01	0.08	0.03
replum apex	0.00	0.02	0.01	0.09	0.35	0.30	0.61	0.93	0.67
replum base	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.77	0.29
trich.: style-base	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
trich.: out. valve	0.00	0.07	0.03	0.76	1.00	0.88	1.00	1.00	1.00
trich.: inn. valve	0.00	0.00	0.00	0.09	0.69	0.59	0.86	1.00	0.95
trich.: replum	0.00	0.07	0.03	0.00	0.06	0.02	0.00	0.05	0.01
trich.: bulbous	0.00	0.00	0.00	0.28	0.85	0.60	1.00	1.00	1.00
trich.: nonbulb.	0.00	0.07	0.03	0.05	0.40	0.19	0.00	0.11	0.03
trich.: nonstalk.	0.00	0.00	0.00	0.54	0.95	0.68	0.41	1.00	0.90
trich.: stalked	0.00	0.00	0.00	0.36	0.66	0.51	0.12	0.84	0.71
trich. type: inn.	0.00	0.00	0.00	0.36	1.42	1.23	1.76	2.00	1.92
silique apex	1.82	1.83	1.82	0.13	0.18	0.13	0.00	0.00	0.00
pedicel length	0.88	1.00	0.94	1.02	1.13	1.05	0.87	1.05	0.94
pedicel no.	1.11	1.50	1.32	1.46	1.75	1.66	1.11	1.68	1.33
trich.>.48 mm.	0.00	0.00	0.00	0.37	0.85	0.64	1.00	1.00	1.00
trich. .16–.48 mm.	0.00	0.00	0.00	0.60	0.72	0.68	0.07	1.00	0.81
trich.<.16	0.00	0.07	0.03	0.46	0.97	0.64	0.41	1.00	0.90

TABLE 10. DATA FROM L. LYRATA, L. DENSIPILA AND THEIR F_2 PROGENIES

	lyrata N=130			*lyrata* × *densipila* N=546			*densipila* N=678		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00
style length	1.71	1.84	1.77	1.63	2.26	1.87	1.59	1.92	1.73
replum length	3.22	3.38	3.30	3.51	4.36	3.90	3.06	3.61	3.37
replum width	3.29	3.46	3.37	3.07	3.43	3.19	3.11	3.53	3.19
silique width	3.62	3.65	3.63	3.38	4.20	3.65	3.03	3.90	3.51
septum perfor.	0.00	0.03	0.02	0.00	0.28	0.03	0.00	0.07	0.02
replum apex	0.00	0.02	0.01	0.29	0.42	0.35	0.00	0.63	0.27
replum base	0.00	0.00	0.00	0.10	0.34	0.25	0.00	0.62	0.24
trich.: style-base	0.00	0.00	0.00	0.19	0.34	0.27	0.12	1.00	0.73
trich.: out. valve	0.00	0.07	0.03	0.66	0.81	0.74	1.00	1.00	1.00
trich.: inn. valve	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.04	0.01
trich.: replum	0.00	0.07	0.03	0.61	0.75	0.70	0.97	1.00	0.99
trich.: bulbous	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
trich.: nonbulb.	0.00	0.07	0.03	0.03	0.20	0.12	1.00	1.00	1.00
trich.: nonstalk	0.00	0.00	0.00	0.66	0.81	0.73	0.00	0.95	0.31
trich.: stalked	0.00	0.00	0.00	0.01	0.47	0.05	0.00	0.54	0.16
trich. type: inn.	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.11	0.03
silique apex	1.82	1.83	1.82	1.00	1.33	1.10	0.98	1.72	1.19
pedicel length	0.88	1.00	0.94	0.92	1.14	0.98	0.79	1.18	0.95
pedicel no.	1.11	1.50	1.32	1.64	1.85	1.74	1.31	1.58	1.49
trich.>.48 mm.	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.01	0.00
trich. .16–.48 mm.	0.00	0.00	0.00	0.00	0.67	0.05	0.00	0.30	0.08
trich.<.16	0.00	0.07	0.03	0.66	0.81	0.73	1.00	1.00	1.00

TABLE 11. DATA FROM L. LESCURII, L. DENSIPILA AND THEIR F_2 PROGENIES

	lescurii N=324			*lescurii* × *densipila* N=608			*densipila* N=678		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$
flower color	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00
style length	1.43	1.74	1.57	1.48	2.31	2.00	1.59	1.92	1.73
replum length	4.50	5.04	4.68	3.83	5.01	4.59	3.06	3.61	3.37
replum width	3.36	3.88	3.75	3.38	4.30	3.99	3.11	3.53	3.19
silique width	1.51	2.01	1.68	2.75	3.95	3.49	3.03	3.90	3.51
septum perfor.	0.01	0.08	0.03	0.00	0.10	0.16?	0.00	0.07	0.02
replum apex	0.61	0.93	0.67	0.89	1.00	0.99	0.00	0.63	0.27
replum base	0.00	0.77	0.29	0.50	1.00	0.93	0.00	0.62	0.24
trich.: style-base	0.00	0.00	0.00	0.00	1.00	0.37	0.12	1.00	0.73
trich.: out. valve	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
trich.: inn. valve	0.86	1.00	0.95	0.00	0.89	0.60	0.00	0.04	0.01
trich.: replum	0.00	0.05	0.01	0.50	1.00	0.89	0.97	1.00	0.99
trich.: bulbous	1.00	1.00	1.00	0.00	1.00	0.46	0.00	0.00	0.00
trich.: nonbulb.	0.00	0.11	0.03	0.50	1.00	0.73	1.00	1.00	1.00
trich.: nonstalk.	0.41	1.00	0.90	0.15	1.00	0.77	0.00	0.95	0.31
trich.: stalked	0.12	0.84	0.71	0.70	1.00	0.90	0.00	0.54	0.16
trich. type: inn.	1.76	2.00	1.92	0.00	2.00	1.21	0.00	0.11	0.03
silique apex	0.00	0.00	0.00	0.00	0.50	0.26	0.98	1.72	1.19
pedicel length	0.87	1.05	0.94	0.63	0.95	0.86	0.79	1.18	0.95
pedicel no.	1.11	1.68	1.33	1.21	2.00	1.65	1.31	1.58	1.49
trich.>.48 mm.	1.00	1.00	1.00	0.00	0.40	0.10	0.00	0.01	0.00
trich. .16–.48 mm.	0.07	1.00	0.81	0.67	1.00	0.79	0.00	0.30	0.08
trich.<.16	0.41	1.00	0.90	0.98	1.00	1.00	1.00	1.00	1.00

can say is that 3 of every 4 populations sampled in 1953 were still in the same place ten or more years later.

There are long stretches of the river where no hybrids are to be found. The larger populations appear to be on low-lying ground on the upper side of long river bends. This suggests that the seeds tend to settle out in areas of quiet water at a time when the river is at flood stage. The river follows a tortuous course, providing many places which seem ideal for the development of hybrid populations, but all such places are not occupied. This may be due to poor dispersal, or it may be that the flood plain is a marginal habitat for these plants.

The seeds have no special dispersal mechanism. They are flat, round and very light in weight. When the capsules mature, the seeds fall to the ground, usually within inches of the mother plant. In this respect, some observations made in Ann Arbor are of interest. In the spring of 1967, F_2 hybrid plants of the *Lesquerella lescurii* × *L. densipila* cross were planted in rows 4 feet apart, with the plants spaced a foot from each other. One inflorescence was harvested from each plant for analysis, but several others remained. No cultivation was performed in the field which was soon overrun by agricultural weeds, largely plants of *Amaranthus*. In the fall, after the annual weeds had died, seedlings of *Lesquerella* were discovered. In the spring of 1968, the number of seedlings surrounding a number of previously selected and marked plants was counted, their distance to the site of the original mother plant measured and the amount of dry matter weighed. The results are depicted in Fig. 3 and given in Table 14. It can be seen that seeds were dispersed only 10–15 inches from the mother plant, most seedlings lying within 5 inches. Those seedlings that lay further away produced the largest plants and the largest number of seeds. In the summer of 1968 the field was plowed and used as an experimental field for other projects. Nevertheless, *Lesquerella* plants germinated in the fall, and in the spring of 1969 a uniform and dense crop of plants was found in the area. No plant was found, however, beyond five feet of the original plot. The cultivation of the field had resulted in a more uniform distribution of the seeds, but even so, few seeds had been dispersed out of the original area.

Statistical problems. As stated previously, 28 populations were sampled over a period of 13 years from a total of eighteen sites. Ideally, a statistic is wanted that would provide an index of the amount and direction of change over all characters for the parameter time, and the parameter distance downstream. Unfortunately, we have not found a statistical procedure that would properly handle our data. Furthermore, statistics that could be applied to a character at a time, such as a two-way analysis of variance or a discriminant function, cannot be applied because only some localities have been sampled more than one year, and no two localities were sampled over the same number of years. This is largely due to the fact that the early sampling was done when we were still trying to

demonstrate the existence of hybridization and no thought had been given to the statistical implications of the sampling procedure. Furthermore, as stated before, the populations themselves are somewhat transient. We have therefore resorted to the following four way analysis in order to discover whether any trends exist: (1) a qualitative description of the direction of change for each character in the populations; (2) a Prim diagram, which shows the phenetic relations of all populations; (3) an analysis of the character by character simple correlation coefficients of all populations; (4) a hybrid index.

Qualitative character by character description (see Table 1)

Flower color (Character No. 1). Both parents have yellow flowers and so do all the hybrid populations.

TABLE 12. GEOGRAPHICAL LOCATION OF WILD POPULATIONS SCORED

Species	Collection Number*	Location of Population
L. densipila		Alabama
	Rollins 57140	Lawrence Co.: 8 mi. east of Wren
	Rollins 5987	Morgan Co.: 5 mi. west of Falkville
	Rollins 6422	Morgan Co.: 5 mi. west of Falkville
		Tennessee
	Rollins 55124	Rutherford Co.: 1.3 mi. southwest of Bethel near the west fork of the Stones River
	Rollins 53138	Williamson Co.: Kirkland
	Rollins & Solbrig 6656	Williamson Co.: just south of Kirkland
	Rollins & Solbrig 6660	Williamson Co.: ¼ mi. from the Harpeth River at the junction of Trinity Rd. and Co. 6183
L. lescurii		Tennessee
	Rollins & Solbrig 6671	Cheatham Co.: 2 mi. west of Ashland City
	Rollins 53134	Davidson Co.: flood plain south of the Harpeth River at Linton
	Rollins 6475	Williamson Co.: 1 mi. east of Arrington
	Rollins & Solbrig 6657	Williamson Co.: ½ mi. south of Arrington
L. lyrata		Alabama
	Rollins 5599	Franklin Co.: 7 mi. east of Russellville
	Rollins 5981	Franklin Co.: 7 mi. east of Russellville and ½ mi. north of Cherry Hill Crossing
L. perforata		Tennessee
	Rollins 53139	Wilson Co.: 5 mi. north of Lebanon near Spring Creek
	Rollins 55141	Wilson Co.: 3 mi. west of Lebanon on US 70N
	Rollins 55145	Wilson Co.: ½ mi. west of Lebanon
	Rollins & Solbrig 6673	Wilson Co.: north of Lebanon near Spring Creek
	Rollins & Solbrig 6674	Wilson Co.: northwest edge of Lebanon
L. stonensis		Tennessee
	Rollins 55138	Rutherford Co.: where Tenn. 102 crosses the east fork of the Stones River
	Rollins 59120	Rutherford Co.: 1 mi. southwest of Lascassas
	Rollins 6147	Rutherford Co.: 1.5 mi. north of Walterhill
	Rollins 6462	Rutherford Co.: Stones River crossing at Lascassas

*Voucher specimens have been placed in the Gray Herbarium.

Style length (Character No. 2). *Lesquerella densipila* has a slightly longer style (1.59–1.92, $\bar{x}$=1.73, (see Table 11 and Figure 4) than *L. lescurii* (1.43–1.74, $\bar{x}$=1.57). The artificial hybrids showed slight overdominance for this character, possibly due to the better culturing conditions of the garden. The natural hybrids varied from a low mean of 1.55 for population 1966–2′, to a high of 1.95 for population 1964–8′. In general, there are more populations (21) with a mean higher than 1.65 (halfway between both parents) than below (5) while 2 have exactly 1.65. Also, the populations downstream are consistently more likely to have means over 1.65, while upstream there is a great deal of fluctuation. The standard

TABLE 13. LOCALITIES IN TENNESSEE, SITE NUMBERS AND COLLECTION NUMBERS FOR WILD POPULATIONS OF HYBRIDS. SEE MAP, FIG. 1

1. Lesquerella densipila × L. lescurii

Site No.	Collection No.	Location of Population
1	Rollins 55115 " 6474	Williamson Co.: just below junction of Arrington Creek and the Harpeth River, SW side of river.
2	Rollins & Solbrig 6658 " & " 6659	Williamson Co.: opposite side of river from site 1.
3	Rollins & Solbrig 6660	Williamson Co.: near junction of Trinity Road and Arno Road, ca. ¼ mile south of the Harpeth River.
4	Rollins & Solbrig 6661	Williamson Co.: NE side of the Harpeth River, just below Trinity Road.
5	Rollins & Solbrig 6662	Williamson Co.: SW side of the Harpeth River near the crossing of Arno Road.
6	Rollins & Solbrig 6664	Williamson Co.: below bridge where interstate route 65 crosses the Harpeth River.
7	Rollins 6507	Williamson Co.: N side of Harpeth River, about 3 miles east of Franklin.
8	Rollins 53135 " 6471 " 6472	Williamson Co.: S side of Harpeth River, 2 miles E of Franklin.
9	Rollins & Solbrig 6666	Williamson Co.: near Harpeth River below bridge where Hillsboro Road crosses the river.
10	Rollins 6514	Williamson Co.: near the Harpeth River where Snead Road crosses the river.
11	Rollins 53133 " 55126 " 6508 Rollins & Solbrig 6663	Davidson Co.: near Harpeth River just below bridge where state route 100 crosses the river.
12	Rollins 55127	Davidson Co.: near Harpeth River, ½ mile southwest of Bellview Post Office.
13	Rollins & Solbrig 6667	Davidson Co.: just below bridge where interstate route 40 crosses the Harpeth River.
14	Rollins 55129*	Davidson Co.: flood plain of Harpeth River, 3 miles W of junction of routes US 70N and US 70S.
15	Rollins 53130	Cheatham Co.: 9 miles E of White Bluff, flood plain of Harpeth River.
16	Rollins 53128 " 55130 " 6477 Rollins & Solbrig 6668	Cheatham Co.: near Harpeth River about 2 miles above bridge where US 70 crosses the river.
17	Rollins 6473 Rollins & Solbrig 6669	Cheatham Co.: above bridge where White Bluff-Ashland City road crosses the Harpeth River.
18	Rollins & Solbrig 6670	Cheatham Co.: below bridge where state route 49 between Ashland City and Charlotte crosses the Harpeth River.

2. Lesquerella densipila × L. stonensis

Site No.	Collection No.	Location of Population
1	Rollins 55175	Rutherford Co.: near Old Jefferson and just above junction of East and West forks of Stones River.
2	Rollins & Solbrig 6652	Davidson Co.: large bend of Stones River at end of Walker Road.
3	Rollins 55166 " 6509 " 6518 Rollins & Solbrig 6649	Davidson Co.: near Stones River, 4 miles NE of Lavergne.
4	Rollins 55171 " 6140 Rollins & Solbrig 6651	Davidson Co.: below and above bridge where Couchville Pike crosses Stones River.
5	Rollins & Solbrig 6653	Davidson Co.: flood plain of Stones River, ½ mile SW of Suggs Creek.
6	Rollins & Solbrig 6654	Davidson Co.: E side of Stones River off Cooke Road.
7	Rollins & Solbrig 6655	Davidson Co.: old corn field, 1 mile below site 6, off Cooke Road.
8	Rollins & Solbrig 6650	Davidson Co.: ¼ mile below bridge of interstate 40 crossing over Stones River.

*Studied but not scored or included in the data tables.

deviation varies between .25 and .36 and the coefficient of variation between 15% and 22%. The comparable values of the F_2 garden populations were s=.42 and cv=21%, indicating no loss of variation in the field populations.

Replum length (Character No. 3). This is one of the characters that best discriminates the two species. *Lesquerella lescurii* has a long replum (4.50–5.04 mm., $\bar{x}$=4.68) while *L. densipila* has a short one (3.06–3.61, $\bar{x}$=3.37). The artificial F_2 hybrid was intermediate but close to the larger parent (3.83–5.01, $\bar{x}$=4.89) again probably due to cultural conditions.

The natural hybrids varied from a low of 3.61 to a high of 4.93. About half the populations (21) had values below 4.00, the rest (17) having values above 4.00. The populations downstream again showed, in general, larger replums than the ones upstream which were likely to show greater differences from site to site. No appreciable difference existed in the standard deviation in most populations (values of .40 to .60). However, two populations had low values (s=.32, .38) and two very high (s=.75 and .76, see Table 15). The coefficient of variation varied from 11% to 16% with two populations showing low values of 8% to 10%. These values are equivalent to the parental populations (s=.57–.65, cv=14%–17%) and the artificial F_2 hybrids (s=.60, cv=13%) indicating no appreciable loss of variation in the natural hybrids.

Replum width (Character No. 4). This is not a good discriminating character between the parents (Fig. 5). *Lesquerella lescurii* has a slightly wider replum (3.36–3.88, $\bar{x}$=3.75) than *L. densipila* (3.11–3.53, $\bar{x}$=3.19). The artificial hybrids showed marked overdominance (3.38–4.30, $\bar{x}$=3.99). See Fig. 5.

In the natural hybrid populations, a great deal of variation for this character was observed, from a low mean of 2.84 to a high of 4.01, that is,

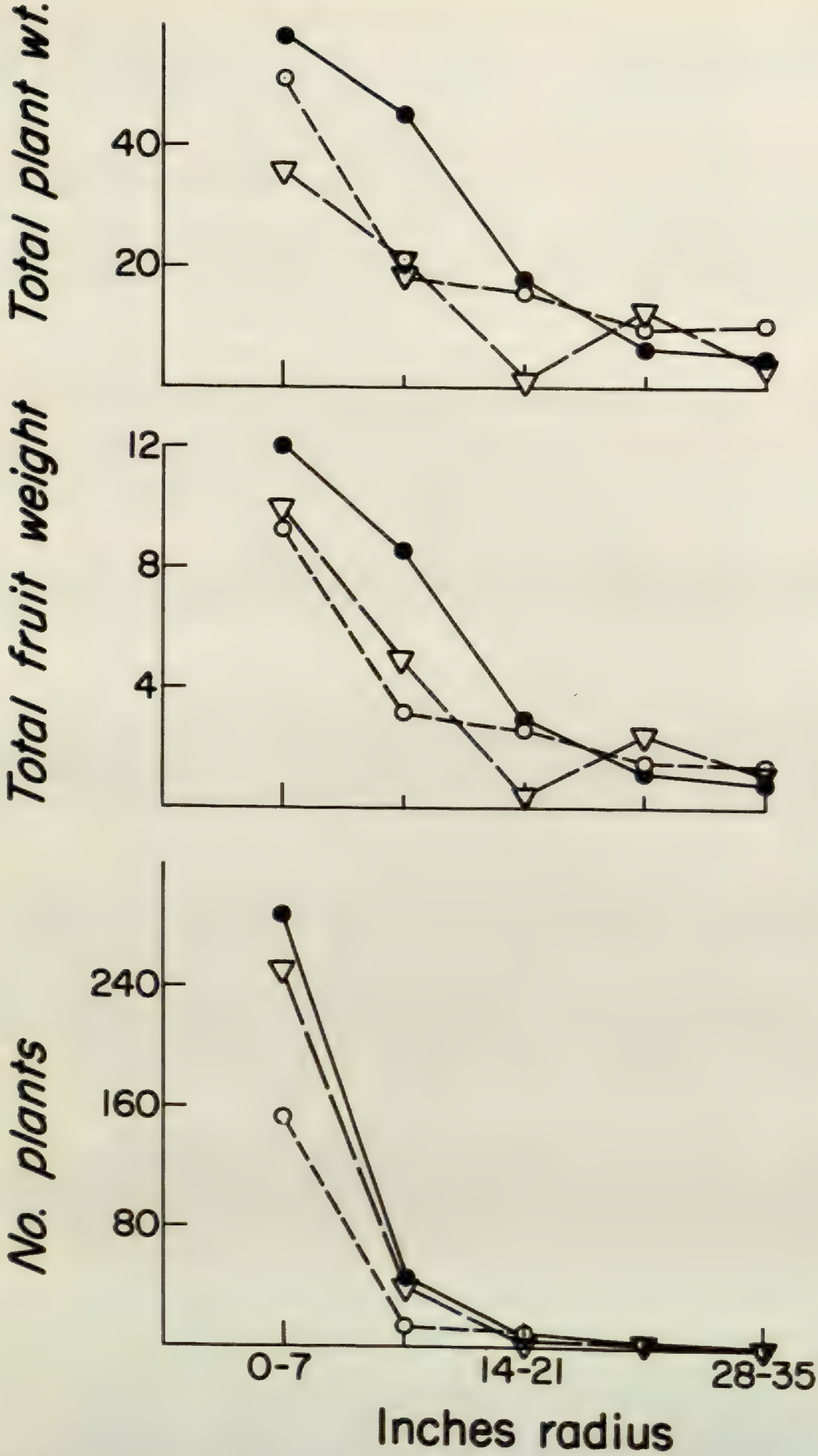

FIG. 3. Progeny plants, fruit weight and plant weight in grams plotted against distance from the three parent plants.

from considerably smaller than *Lesquerella densipila* to considerably larger than *L. lescurii*, as well as slightly larger than the artificial F_2 plants. This variation is also shown by the standard deviation (.31–.53), and the coefficient of variation (9%–17%). The corresponding values of *L. lescurii* are s–.49, cv=13%; for *L. densipila*, s=.49, cv=15% and for the artificial F_2, s=.40, cv=10%. Again, as with previous characters, the populations downstream show a tendency to have larger values while those upstream are quite variable. Why this character shows such a range in variability we cannot say.

Silique width (Character No. 5). This is the most discriminating character between the two species. *Lesquerella lescurii* has a flat silique while *L. densipila* has a globose one. Since the capsule of *L. lescurii* is larger, the actual thickness measurement differences are not as great as the "gestalt" differences. The mean thickness for true populations of *L. lescurii* is 1.68 mm. (1.51–2.01) while that of *L. densipila* is 3.51 (3.03–3.90); the artificial F_2 has a value of 3.49 (2.75–3.95) similar to that of the largest parent (Fig. 6).

In the natural hybrid populations, again a great deal of variation is encountered, from a low mean of 1.62 to a high of 3.82, compared to values observed in the parental populations. These values were all obtained from data taken on upstream populations. With variance from a low of s=.38 to a high of s=.63, the coefficient of variation varies from 13% to 27%, that is, twice as much. Thus, a great many rearrangements are indicated for this character. Therefore, it is of interest that the populations downstream from population 9 have more similar means (2.49–3.31) and coefficients of variation (15% to 23%) than those above it.

Silique length/width ratio. The silique length/width ratio is probably a better indicator than width alone as to similarity to either parent because it eliminates the effects of luxuriance. The length/width ratio of *Lesquerella lescurii* is 2.80; for *L. densipila* it is 0.96; and for the artificial F_2 hybrid, 1.65. In the natural hybrid populations, the lowest value observed was 1.06, the highest 2.40. That is, no population transcended its parents, confirming that they are all intermediates to a lesser or greater degree.

TABLE 14. NUMBER OF SEEDLINGS, FRESH WEIGHT, AND FRUIT WEIGHT OF NATURALLY DISPERSED LESQUERELLA DENSIPILA × L. LESCURII SEEDLINGS

	Distance in cm. from mother plant				
A. Number of plants	0–7	7–14	14–21	21–28	28–35
Plant 1	288	139	28	14	7
Plant 2	252	125	8	51	10
Plant 3	155	46	50	13	7
B. Total fresh weight (g.)					
Plant 1	57.8	136.2	90.4	48.4	46.5
Plant 2	36.2	65.6	6.3	90.7	40.9
Plant 3	53.1	56.5	29.4	69.7	95.9
C. Fruit weight (g.)					
Plant 1	12.1	25.6	14.5	8.4	6.9
Plant 2	9.7	14.7	2.0	16.9	9.0
Plant 3	9.3	9.5	13.5	10.8	12.7

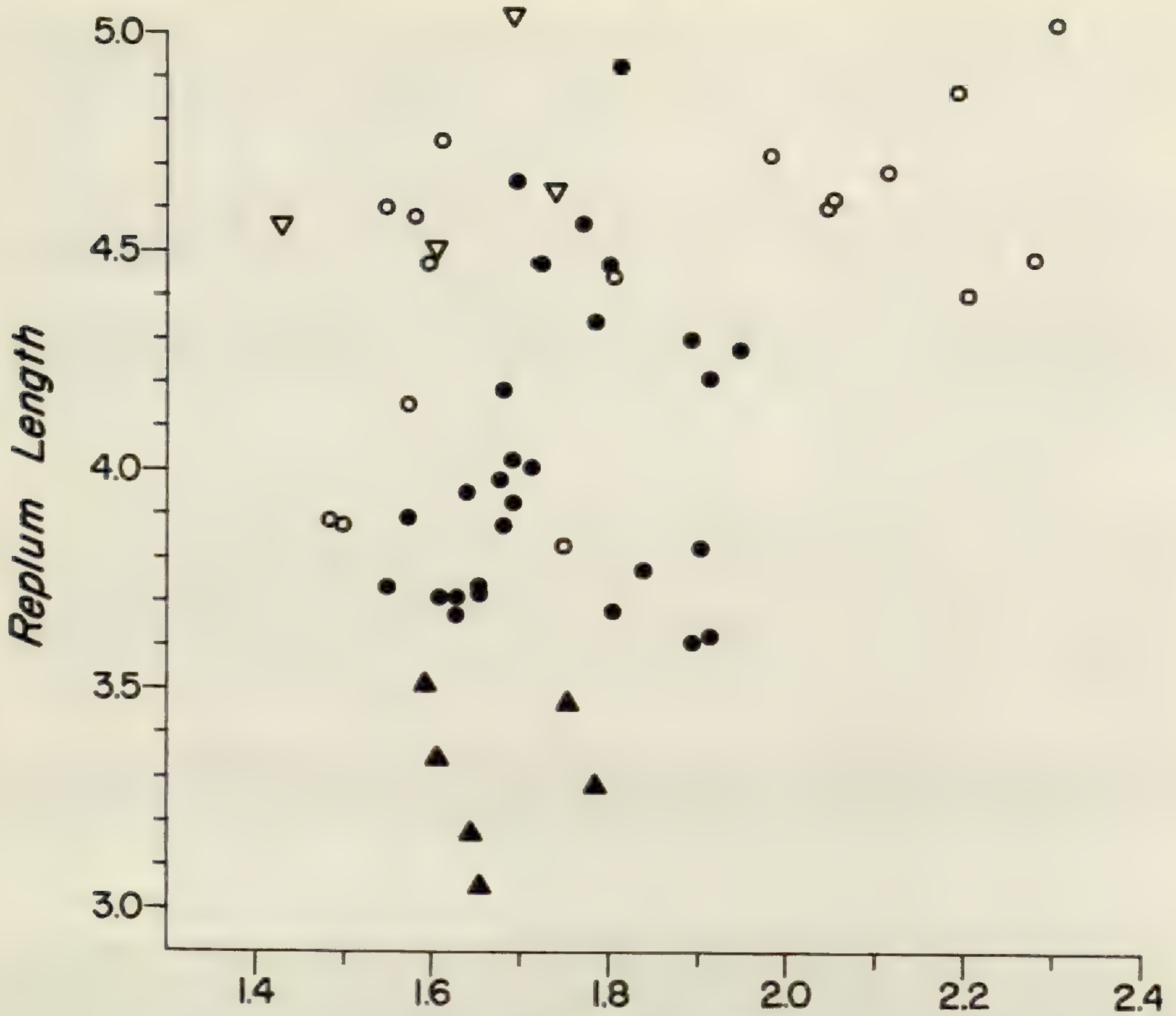

FIG. 4. Mean replum length (mm.) vs. mean style length (mm.) in populations of *Lesquerella*. Solid triangles: *L. densipila*. Open triangles: *L. lescurii*. Solid circles: *L. densipila* × *L. lescurii*, field populations. Open circles: *L. densipila* × *L. lescurii*, garden populations.

However, the more interesting point is that the populations upriver (sites 2–13) show a great deal of variation (1.06–2.40) while those downstream are rather uniform (1.40–1.70). At the junction of the upper Harpeth River and Arrington Creek, the following values were obtained at the three sites sampled (1,2,2′): 1955 (1) 1.50; 1964 (1) 1.10; 1966 (2)2.40; 1966 (2′) 1.93.

Septum perforation (Character No. 6). Both parents have basically unperforated septa as do the hybrid populations. Occasional perforated septa in some plants may be due to stresses during the drying of the material.

Replum apex (Character No. 7). This is another distinctive character that separates these two species but it is difficult to score because some subjectivity is involved. In *Lesquerella densipila* the replum apex is rounded (Fig. 2) scored as 0, and in *L. lescurii* it is pointed (scored as 1). Scoring each plant as 1 or 0, with mean values varying from 0 to 0.63 were found to obtain in wild populations of *L. densipila* (with a grand mean for the species of 0.27), while in populations of *L. lescurii* the corresponding values were 0.61 and 0.93 (species mean 0.67). Artificial

garden hybrids always had a pointed replum apex (mean for all plants 0.99). The natural hybrids, however, showed a great deal of variation, from populations with all rounded apices (value of .04) to all pointed (value of 1.00). Of the 27 populations analyzed, only 8 had values that can be considered intermediate (range of 0.30 to 0.65). It is our feeling, in view of the results of both the garden studies and the field studies, that this character has a big environmental component in its expression. Consequently, although it is very adequate to separate the parent species, it is not very useful as an indicator in hybrid populations. This is further reinforced when the variance values are analyzed. The standard deviation values vary from 0.00 to 0.50; the coefficient of variation from 0% to 466.83%!

Replum base (Character No. 8). What has been said of the replum apex applies as well to the base. Furthermore, there is no substantial difference between the parent populations in this character.

Trichomes at the base of the style (Character No. 9). *Lesquerella lescurii* has no trichomes at the base of the style while they are nearly always present in *L. densipila*. Segregation of this character in the F_2 population is controlled by more than one gene. The overall mean for the F_2 population was 0.37. Field hybrids varied from populations entirely lacking plants with trichomes at the base of the style (pop. 53–11) to those where every plant had them present (pop. 65–10). However, the majority of the populations were intermediate for this character. Populations markedly *densipila*-like, that is, with trichomes at the base of the style in the majority of the plants, were found only upstream and were in the minority; most populations either had a more or less even mixture or a majority of the plants were without trichomes at the base of the style. The latter were found mostly downstream. With respect to this character, there is a tendency for the populations to become more *lescurii*-like farther downstream. Values for standard deviation and coefficient of variation are not too meaningful because of the bimodal distribution of the character in the population.

Trichomes on the outer surface of the valve (Character No. 10, 13, 16, 21–23). Both species have trichomes on the outer surface of the fruit valve. However, the trichomes of *Lesquerella densipila* are mostly simple, while those of *L. lescurii* are a mixture of unbranched trichomes with bulbous bases, and others that are dendritically branched. Artificial hybrids are intermediate in their indumentum, having all three types of trichomes. Natural hybrid populations show the same situation. Twenty-five per cent (pop. 64–17) to 100 per cent of the plants have simple trichomes and 13–90 per cent have branched ones, except population 64–1, where 2 per cent of the plants had branched trichomes. A slight tendency for the plants to become more *lescurii*-like downstream can be seen in the relative increase in the percentage of plants with branched trichomes in the populations farther downstream.

TABLE 15. MEAN VALUES FOR CHARACTERS OF FIELD HYBRIDS OF L. LESCURII × L. DENSIPILA

Character	Site 55–1		64–1		66–2		66–2′		66–3	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
1	5.00	.00	5.00	.00	5.00	.00	5.00	.00	5.00	.00
2	1.60	.33	1.69	.37	1.57	.29	1.55	.31	1.92	.34
3	3.72	.56	4.02	.52	3.89	.53	3.73	.55	3.61	.57
4	3.33	.40	3.65	.51	2.95	.44	2.84	.49	3.11	.38
5	2.49	.63	3.82	.51	1.63	.43	1.93	.53	3.43	.45
6	0.02	.14	0.00	.00	0.07	.26	0.08	.28	0.02	.14
7	0.28	.45	0.12	.32	0.74	.44	0.69	.48	0.63	.48
8	0.00	.00	0.00	.00	0.82	.39	0.82	.39	0.62	.49
9	0.18	.39	0.67	.47	0.07	.26	0.07	.25	0.76	.43
10	1.00	.00	1.00	.00	1.00	.00	1.00	.00	1.00	.00
11	0.48	.50	0.00	.00	0.90	.30	0.74	.44	0.04	.20
12	0.62	.49	1.00	.00	0.44	.50	0.58	.50	0.97	.16
13	0.26	.44	0.00	.00	0.87	.34	0.57	.00	0.00	.00
14	0.83	.38	1.00	.00	0.56	.50	0.68	.47	0.99	.07
15	0.74	.44	0.02	.14	0.96	.19	0.86	.36	0.30	.46
16	0.66	.48	0.00	.00	0.80	.40	0.86	.36	0.54	.50
17	1.09	1.20	0.00	.00	2.02	.79	1.94	1.20	0.11	.54
18	0.44	.50	1.03	.55	0.00	.00	0.05	.22	0.98	.18
19	0.84	.22	1.10	.22	0.83	.21	0.77	.18	0.97	.20
20	1.50	.15	1.23	.21	1.16	.26	1.22	.22	1.58	.36
21	0.37	.49	0.00	.00	0.97	.16	0.84	.37	0.01	.10
22	0.73	.45	0.03	.17	0.82	.39	0.87	.34	0.30	.46
23	1.00	.00	1.00	.00	0.99	.09	1.00	.00	1.00	.00

Character	Site 66–4		66–5		66–6		65–7		53–8	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
1	5.00	.00	5.00	.00	5.00	.00	5.00	.00	5.00	.00
2	1.89	.32	1.81	.34	1.63	.32	1.66	.31	1.68	.34
3	3.61	.61	3.67	.58	3.67	.52	3.75	.50	3.97	.57
4	3.02	.47	3.12	.42	3.07	.41	3.46	.33	3.40	.44
5	3.37	.56	3.40	.55	2.50	.52	2.90	.49	2.77	.50
6	0.02	.13	0.09	.28	0.08	.27	0.00	.00	0.08	.27
7	0.81	.40	0.72	.45	0.91	.29	0.04	.21	0.90	.31
8	0.53	.50	0.62	.49	0.76	.43	0.01	.09	0.95	.22
9	0.81	.40	0.50	.50	0.25	.44	0.23	.42	0.14	.35
10	1.00	.00	1.00	.00	1.00	.00	1.00	.00	1.00	.00
11	0.11	.32	0.08	.27	0.46	.50	0.27	.44	0.44	.50
12	1.00	.00	0.95	.23	0.74	.44	0.82	.38	0.57	.50
13	0.00	.00	0.00	.00	0.12	.33	0.01	.09	0.33	.47
14	1.00	.00	1.00	.00	0.94	.24	1.00	.00	0.82	.39
15	0.13	.34	0.21	.41	0.39	.49	0.25	.43	0.29	.46
16	0.26	.44	0.40	.49	0.83	.38	0.29	.46	0.94	.25
17	0.26	.79	0.19	.70	1.17	1.37	0.40	.79	1.09	1.31
18	0.94	.25	0.97	.22	0.18	.39	0.77	.42	0.39	.49
19	1.13	.27	1.13	.22	0.79	.16	1.15	.18	0.91	.20
20	1.40	.36	1.55	.34	1.35	.23	1.32	.23	1.36	.30
21	0.00	.00	0.00	.00	0.23	.42	0.04	.19	0.13	.34
22	0.07	.25	0.02	.15	0.80	.40	0.43	.50	0.70	.46
23	1.00	.00	1.00	.00	1.00	.00	1.00	.00	1.00	.00

TABLE 15. (Continued)

Character	Site 64–8 $\bar{x}$	64–8 s	64–8′ $\bar{x}$	64–8′ s	66–9 $\bar{x}$	66–9 s	65–10 $\bar{x}$	65–10 s	53–11 $\bar{x}$	53–11 s
1	5.00	.00	5.00	.00	5.00	.00	5.00	.00	5.00	.00
2	1.70	.31	1.95	.36	1.65	.30	1.68	.31	1.68	.25
3	4.67	.61	4.27	.76	3.74	.48	3.87	.38	4.18	.32
4	3.92	.48	3.79	.46	3.18	.39	3.14	.37	3.54	.31
5	2.67	.58	3.60	.48	2.70	.49	2.77	.40	2.49	.38
6	0.05	.22	0.00	.00	0.41	.20	0.00	.00	0.00	.00
7	0.33	.47	0.31	.47	0.93	.26	0.04	.19	0.14	.36
8	0.01	.07	0.00	.00	0.78	.42	0.00	.00	0.00	.00
9	0.06	.24	0.63	.49	0.51	.50	1.00	.00	0.00	.00
10	0.99	.07	1.00	.00	1.00	.00	1.00	.00	1.00	.00
11	0.59	.49	0.20	.41	0.49	.50	0.00	.00	0.50	.52
12	0.63	.48	0.97	.17	0.89	.31	1.00	.00	0.14	.36
13	0.41	.49	0.00	.00	0.07	.26	0.00	.00	0.35	.50
14	0.63	.48	1.00	.00	0.99	.09	1.00	.00	0.71	.47
15	0.78	.42	0.23	.43	0.26	.44	0.30	.47	0.71	.47
16	0.44	.50	0.00	.00	0.93	.26	0.04	.19	0.21	.43
17	1.20	1.15	0.20	.41	1.28	1.40	0.00	.00	1.36	1.39
18	0.19	.40	0.91	.45	0.64	.48	1.00	.00	0.36	.50
19	1.08	.22	1.13	.22	0.81	.16	1.15	.17	0.94	.22
20	1.24	.24	1.40	.28	1.51	.28	0.92	.13	1.10	.17
21	0.38	.49	0.00	.00	0.17	.38	0.00	.00	0.07	.27
22	0.86	.35	0.23	.43	0.71	.46	0.19	.40	0.71	.47
23	1.00	.00	1.00	.00	1.00	.00	1.00	.00	1.00	.00

Character	Site 55–11 $\bar{x}$	55–11 s	65–11 $\bar{x}$	65–11 s	66–11 $\bar{x}$	66–11 s	55–12 $\bar{x}$	55–12 s	66–13 $\bar{x}$	66–13 s
1	5.00	.00	5.00	.00	5.00	.00	5.00	.00	5.00	.00
2	1.84	.31	1.62	.28	1.91	.35	1.73	.28	1.92	.33
3	3.78	.42	3.71	.47	3.83	.59	4.01	.64	4.21	.64
4	3.26	.38	3.32	.37	3.27	.40	3.55	.50	3.39	.43
5	2.86	.52	2.59	.38	3.31	.48	2.77	.58	2.49	.50
6	0.00	.00	0.03	.18	0.06	.23	0.08	.28	0.04	.22
7	1.00	.00	0.07	.26	0.83	.38	0.23	.43	0.63	.48
8	0.92	.28	0.00	.00	0.79	.41	0.00	.00	0.64	.48
9	0.45	.50	0.12	.33	0.54	.50	0.10	.31	0.22	.41
10	0.98	.15	1.00	.00	1.00	.00	1.00	.00	1.00	.00
11	0.38	.49	0.53	.50	0.11	.31	0.54	.50	0.53	.50
12	0.72	.36	0.76	.43	0.91	.29	0.71	.46	0.66	.48
13	0.11	.31	0.09	.28	0.00	.00	0.19	.39	0.53	.50
14	0.98	.15	0.98	.13	0.99	.09	0.90	.31	0.82	.39
15	0.21	.41	0.59	.50	0.35	.48	0.63	.50	0.64	.48
16	0.79	.41	0.53	.50	0.60	.49	0.67	.48	0.86	.35
17	0.83	1.17	1.09	1.16	0.23	.73	1.13	1.20	1.27	1.25
18	0.53	.50	0.45	.50	0.91	.29	0.56	.50	0.13	.33
19	0.90	.14	1.07	.14	1.11	.25	0.89	.17	1.06	.22
20	1.36	.26	1.13	.19	1.51	.35	1.30	.25	1.39	.30
21	0.15	.36	0.26	.44	0.01	.09	0.21	.41	0.72	.45
22	0.77	.43	0.90	.38	0.17	.38	0.90	.31	0.98	.15
23	0.98	.15	0.97	.18	1.00	.00	0.98	.14	0.99	.08

TABLE 15. (Continued)

Character	Site 53–15 $\bar{x}$	53–15 s	53–16 $\bar{x}$	53–16 s	55–16 $\bar{x}$	55–16 s	64–16 $\bar{x}$	64–16 s	66–16 $\bar{x}$	66–16 s
1	5.00	.00	5.00	.00	5.00	.00	5.00	.00	5.00	.00
2	1.77	.35	1.65	.36	1.69	.33	1.73	.35	1.89	.29
3	4.56	.75	3.96	.56	3.92	.47	4.47	.50	4.30	.59
4	4.01	.53	3.54	.45	3.36	.46	3.93	.42	3.58	.44
5	3.19	.61	2.36	.54	2.49	.58	2.58	.53	2.74	.59
6	0.02	.13	0.05	.22	0.05	.23	0.01	.12	0.02	.14
7	0.28	.45	0.25	.43	0.90	.30	0.16	.37	0.41	.49
8	0.02	.13	0.00	.00	0.92	.27	0.00	.00	0.57	.50
9	0.03	.18	0.12	.33	0.12	.32	0.07	.25	0.27	.44
10	1.00	.00	1.00	.00	1.00	.00	1.00	.00	1.00	.00
11	0.62	.49	0.62	.49	0.64	.48	0.68	.47	0.65	.48
12	0.31	.47	0.36	.48	0.53	.50	0.21	.41	0.67	.47
13	0.48	.50	0.59	.50	0.53	.50	0.43	.50	0.37	.49
14	0.69	.47	0.57	.50	0.80	.40	0.80	.40	0.90	.30
15	0.92	.28	0.80	.40	0.63	.49	0.91	.29	0.67	.47
16	0.89	.32	0.74	.44	0.88	.32	0.61	.49	0.84	.37
17	1.48	1.26	1.48	1.28	1.46	1.17	1.43	1.02	1.67	1.34
18	0.62	.52	0.13	.34	0.21	.41	0.22	.42	0.09	.29
19	1.02	.25	0.85	.25	0.81	.22	1.06	.17	1.08	.18
20	1.32	.13	1.12	.13	1.57	.37	1.38	.20	1.58	.40
21	0.54	.50	0.64	.48	0.48	.50	0.58	.50	0.62	.49
22	0.98	.13	0.99	.10	0.92	.27	0.96	.20	0.96	.20
23	1.00	.00	1.00	.00	0.99	.09	1.00	.00	0.97	.17

Character	Site 64–17 $\bar{x}$	64–17 s	66–17 $\bar{x}$	66–17 s	66–18 $\bar{x}$	66–18 s
1	5.00	.00	5.00	.00	5.00	.00
2	1.82	.30	1.78	.33	1.81	.32
3	4.93	.61	4.34	.62	4.46	.56
4	4.00	.41	3.53	.44	3.69	.47
5	3.10	.55	2.86	.50	2.50	.58
6	0.04	.20	0.04	.19	0.01	.09
7	0.39	.49	0.92	.28	0.50	.50
8	0.01	.07	0.82	.38	0.67	.47
9	0.10	.30	0.17	.38	0.06	.24
10	1.00	.07	0.99	.09	1.00	.00
11	0.58	.50	0.62	.49	0.54	.50
12	0.61	.49	0.69	.47	0.31	.47
13	0.86	.35	0.31	.47	0.46	.50
14	0.25	.44	0.96	.21	0.75	.44
15	0.77	.42	0.63	.49	0.55	.50
16	0.69	.46	0.88	.32	0.86	.35
17	1.24	1.14	1.53	1.30	1.26	1.24
18	0.09	.29	0.17	.40	0.09	.28
19	1.08	.18	1.07	.20	1.03	.18
20	1.40	.27	1.44	.32	1.45	.38
21	0.65	.48	0.60	.49	0.55	.50
22	0.99	.12	0.93	.25	0.94	.24
23	0.98	.14	0.99	.09	0.97	.16

As for size, the indument of *Lesquerella lescurii* is formed by a mixture of "long" and "medium" simple trichomes, and short branched trichomes, while those of *L. densipila* are exclusively "short" and mostly simple. Artificial F_2 hybrids show a more or less even mixture of "medium" and "short" trichomes. So do the field populations of hybrids. However, as one proceeds downstream, the proportion of plants with "long" trichomes and "medium" trichomes increases steadily. Also, all plants possess some short trichomes in addition.

Trichomes on the inner surface of the valve (Characters 11 and 17). *Lesquerella lescurii* has branched trichomes on the inner surface of the fruit valve, while *L. densipila* is glabrous. Most F_2 artificial hybrids also had branched trichomes on the inner surface of the valve. There is a fair amount of variation in this character in the natural hybrids, where in one population (64–1) no plant had trichomes while in another (66–2) trichomes were present in 90 per cent of the plants.

The between population variation becomes less severe downstream where approximately 60 per cent of the plants in every population have trichomes on the inner surface of the valve.

Trichomes on replum (Character No. 12). *Lesquerella densipila* possesses trichomes on the replum, while *L. lescurii* does not. In artificial F_2 populations most (but not all) plants have trichomes on the replum. The same situation hold for field populations of hybrids but variation is higher here. Once more, populations downstream are less variable for this character than are populations upstream, with a very slight tendency for the populations to become more glabrous.

Silique apex (Character No. 18). Plants of *Lesquerella lescurii* have siliques with an acute apex while those of *L. densipila* are rounded or slightly depressed. Artificial F_2 hybrid populations tend to have either acute or rounded apices. Field populations tend to have either acute or rounded apices. Field populations vary from almost all rounded or depressed to all acute. Once more, populations down river are less varied from site to site than those upstream, and they tend to have a majority of plants with an acute apex.

Infructescence (Character No. 19, 20). The inflorescences of both these species are essentially alike. Consequently no significant difference can be found in pedicel length or number of pedicels in 5 cm. of the inflorescence axis.

Summary of character by character variation. Three features are evident when the variation of the different characters is analyzed. The first is the large differences in the variation patterns both within a population and also from population to population. A second feature is that populations upstream show a greater degree of variation from year to year and from site to site than do populations downstream where, in general, they tend to be more intermediate. Third, a tendency was noted from the populations downstream to become slightly more *lescuri*-like, particularly in characters of the indument.

The Prim diagram. In order to ascertain the degree to which the hybrid populations resemble populations of the parent species, a numerical analysis of all parental populations, natural hybrid populations and artificial F_2 populations was undertaken.

A numerical taxonomic analysis consists of two parts: (1) obtaining a similarity coefficient, e.g., a generalized distance, a coefficient of association or a coefficient of correlation; and (2) the linking together of the OTU (operational taxonomic units) in a two-dimentional graph on the basis of the similarity coefficients obtained in (1). In the present study, the so-called Prim network technique has been used in solving both aspects of the numerical taxonomical problem. The Prim network technique was developed in 1957 by R. C. Prim to determine the shortest possible network of direct links between a given set of telephone terminals. His technique can be applied as well to problems in systematic biology.

As stated above, two major steps are involved in the computational procedure. The first consists in setting up a "distance table" (an $n \times n$ taxa matrix) which gives the distance between all the taxa. The distance measure (D) used here is the sum over all characters of the absolute value of the difference between the character states in taxon A and B.

$$D(A,B)=\sum_{i}|X(A,i)-X(B,i)|$$

where X(A,i) denotes the state of character i for OTU A.

The second step is to connect the various taxa in such a way as to produce the shortest total distance. The detailed instructions for doing this are given by Prim (1957). Basically, the procedure consists of choosing the shortest links connecting any two species, and then by a process of elimination, adding more links until all species are connected in a network. This network can have any form, from completely linear—that is, all species can be arranged in a straight line, to perfectly radial—where all species are connected to a central one.

The Prim network is a graphic representation of closest neighbor relations. It is ideally suited for analyzing graphically hybrid swarms and the degree to which the hybrids resemble the parental populations. Figure 7 depicts the Prim diagram that was obtained. The OTUs are the various field populations of *Lesquerella lescurii* and *L. densipila*, the natural hybrids among them, and the artificial F_2 garden hybrids. The character states used are the mean values of the 23 characters analyzed (Tables 1, 11 and 15) without any further manipulation.

Several interesting features emerge from the graph:

(1) The artificial F_2 hybrids are clumped together and about equidistant from the parental species.

(2) The bulk of the natural hybrids (15/28) are also clumped together, also about equidistantly from the parental species, but separated from the artificial hybrids.

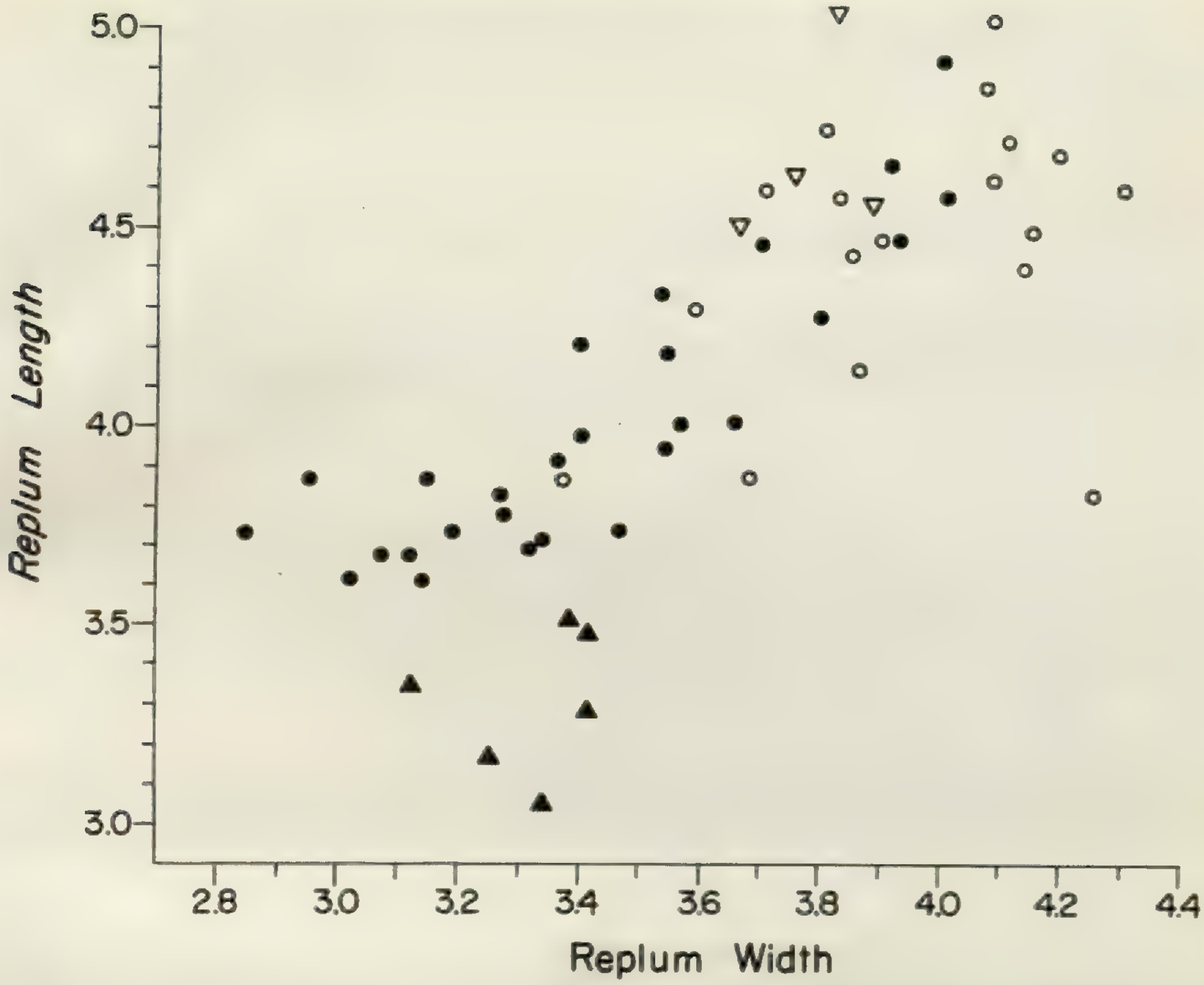

FIG. 5. Mean replum length (mm.) vs. mean replum width (mm.) in populations of *Lesquerella*. Solid triangles: *L. densipila*. Open triangles: *L. lescurii*. Solid circles: *L. densipila* × *L. lescurii*, field populations. Open circles: *L. densipila* × *L. lescurii*, garden populations.

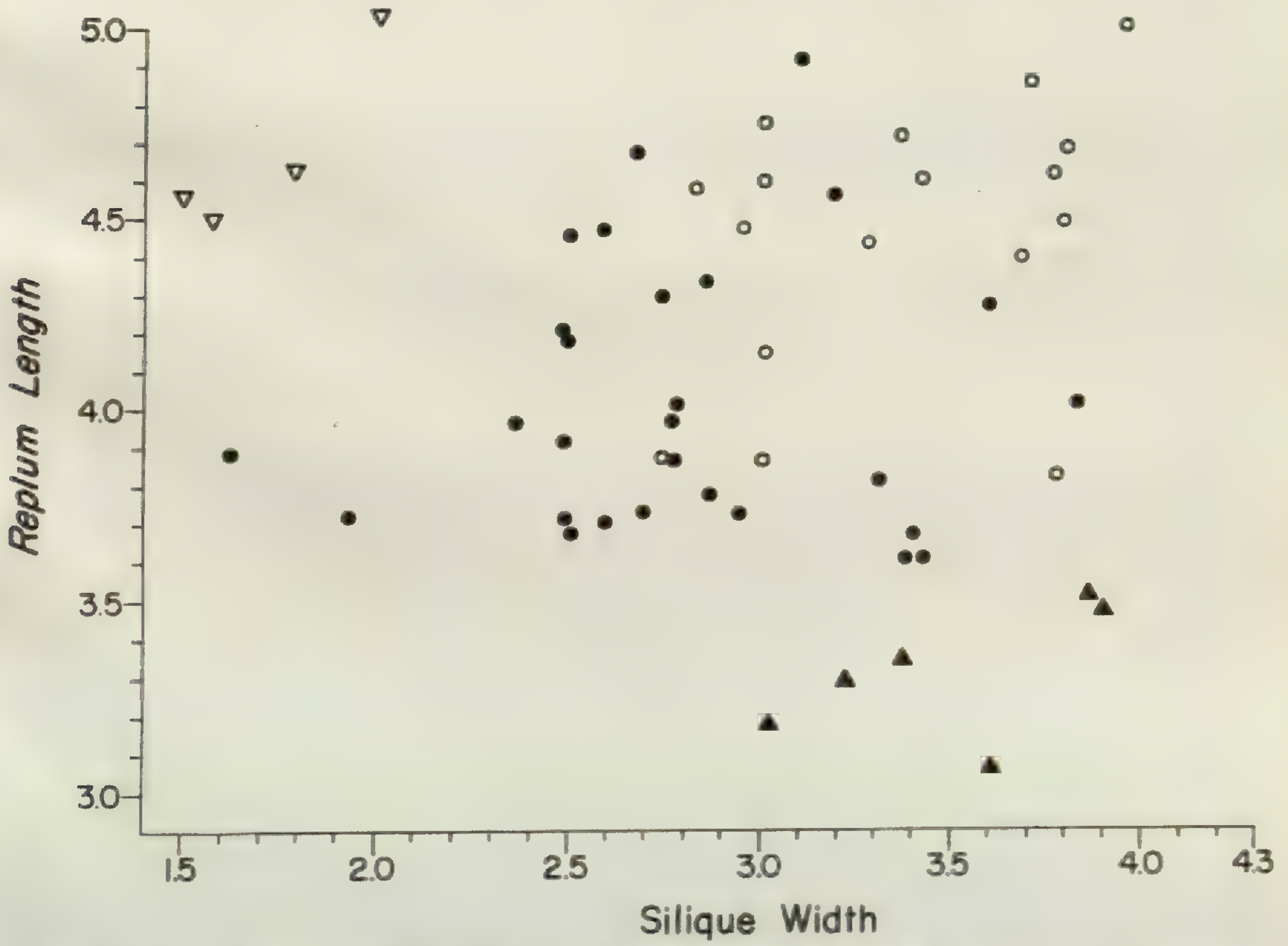

FIG. 6. Mean replum length (mm.) vs. mean silique width (mm.) in populations of *Lesquerella*. Open triangles: *L. lescurii*. Solid triangles: *L. densipila*. Solid circles: *L. densipila* × *L. lescurii*, field populations. Open circles: *L. densipila* × *L. lescurii*, garden populations.

(3) Some populations of natural hybrids (4) are intermediate between the bulk of the hybrids and *Lesquerella lescurii* and are presumed to be introgressants, while others (5) are intermediate between the bulk of the hybrids and *L. densipila* and are also presumed to be introgressants. Finally, four populations of hybrids clump with *L. densipila* and away from the hybrid populations. These are presumed to be true *L. densipila* or introgressants with *L. densipila* strongly predominating and with very few *L. lescurii* characters.

(4) No chronological trend was observed, the distribution among introgressants and intermediates is about the same for populations sampled in 1953, 1955, 1964, 1965 and 1966.

(5) Of the 15 hybrid populations classed as intermediates, eleven were from down river (out of 16 sampled in that area) at least 25 miles away from the place where Arrington Creek meets the Harpeth River, and only four intermediates out of 12 sampled there came from near the junction of these two streams. Among the introgressed populations, 8 came from near this junction and only five were from downriver. Of these, only one was from beyond locality 11, about 25 miles from the junction.

Correlation coefficients. In another section (see Genetic coherence) the reason for this part of the analysis is explained in more detail. In brief, character by character simple correlations were obtained, and their values averaged to obtain a value for the population.

The character by character simple correlation of independent characters in natural populations of true breeding species should be zero or close to it, by definition. However, it was observed by Anderson (1949) and more recently by Clausen (1967) that in hybrids, characters that segregate independently in the parent plants do not necessarily segregate independently in the hybrids. The numerical value of the population obtained by averaging all the correlations can therefore be used as a kind of index of hybridity.

Table 16 shows the values obtained. With the exception of one population (64–1) with a value of .065, all populations had values significantly higher than the parental species, confirming their hybrid nature. The values, however, were lower in general than those of the artificial F_2 hybrids. Furthermore, it can be seen that the populations downstream show much less variability from site to site (.133 to .176) than populations upstream (.065–.221).

Hybrid index. A simple hybrid index was constructed and the populations were scored accordingly (Table 16). It confirmed what the analysis of characters, the Prim diagram, and the correlation coefficient had shown: that populations upstream tended to be more similar to one of the parents (10 of 15) rather than intermediate (5 of 15). The reverse is true of the populations downstream where 6 of 8 populations had an intermediate value of 3 in a scale from 0 to 6, the other 2 having a value of 2, that is, toward *Lesquerella lescurii.*

LESQUERELLA DENSIPILA × L. LESCURII—SUMMARY

At the beginning of this investigation, we addressed ourselves to the following question: is the variation of the hybrid populations greatest near the area where they are formed, or is the variation more or less uniform throughout the area of their occurrence? That is, we were interested in knowing whether natural selection was favoring certain genotypes among the array present in the hybrid swarms upstream. If such were the case, the favored genotypes should be more numerous farther downstream where presumably the influx of genes from the parental species is least intense.

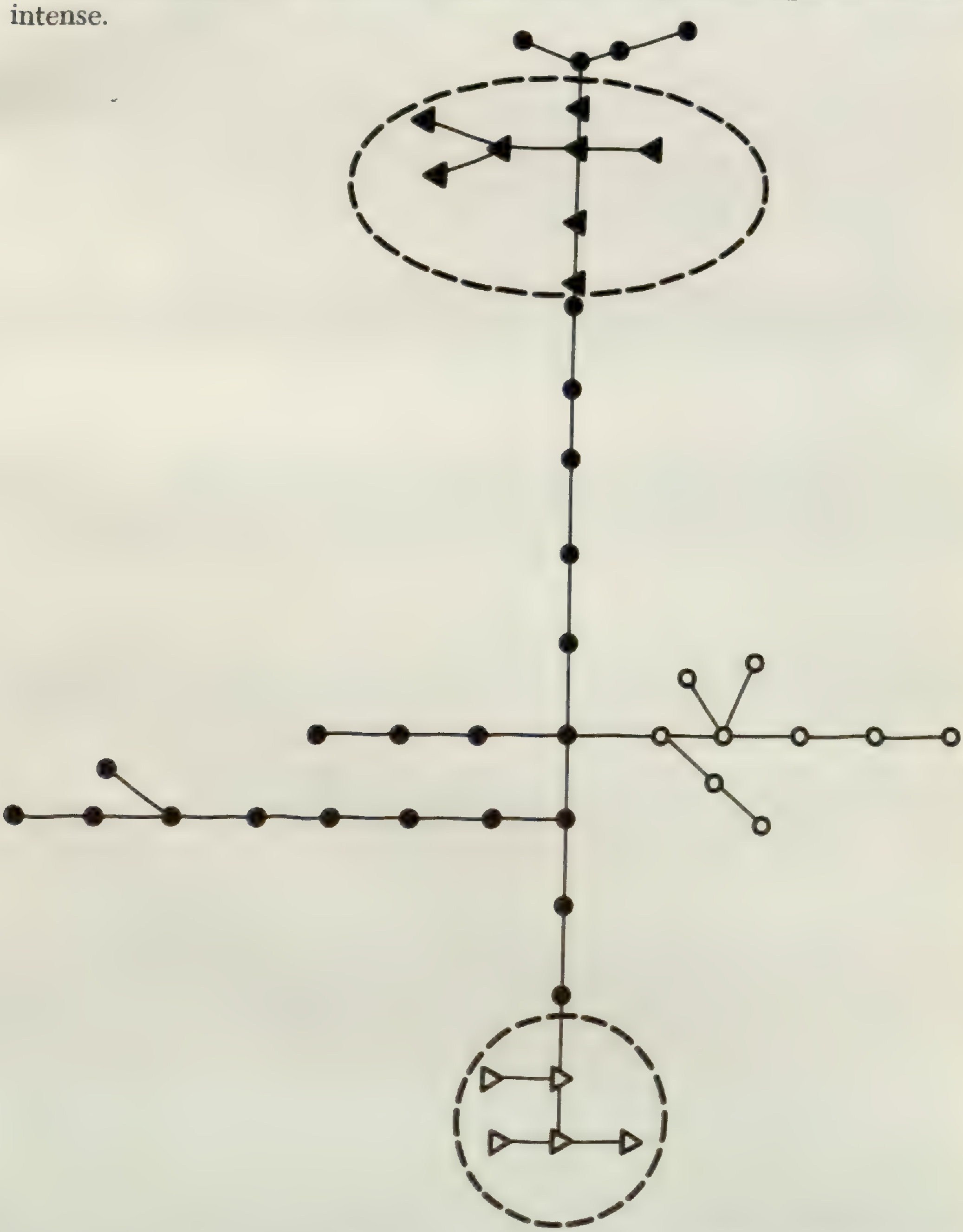

FIG. 7. Prim diagram. Open triangles: *Lesquerella lescurii*. Solid triangles: *L. densipila*. Solid circles: *L. densipila* × *L. lescurii*, field populations. Open circles: *L. densipila* × *L. lescurii*, garden populations.

TABLE 16. AVERAGE OF CORRELATIONS OF ALL CHARACTERS IN WILD POPULATIONS OF L. LESCURII × L. DENSIPILA AND HYBRID INDEX NUMBERS.*

Upstream populations

Correlations .065–.221; index 0–6

Year & locality	Correlations	Index	Year & locality	Correlations	Index
55–1	.221	3	65–7	.131	5
64–1	.065	6	53–8	.172	2
66–2	.151	0	64–8	.181	3
66–2′	.161	0	66–9	.147	3
66–3		6	65–11	.176	4
66–4	.128	5	66–11	.133	4
66–5	.128	5	66–13	.162	3
66–6	.153	3			

Downstream populations

Correlations .156–.177; index 2–3

Year & locality	Correlations	Index	Year & locality	Correlations	Index
53–15	.171	3	53–16	.156	3
66–16	.157	3	66–17	.168	2
64–16	.170	2	64–17	.171	3
55–16	.177	3	66–18	.163	3

*Index numbers, 0–6.
0=lescurii-like.
6=densipila-like.

After carefully studying these populations for a considerable number of years and over their total range of distribution, we find that the populations downstream, taken as a group, are more uniform than those upstream and show a more restricted range of morphological types. However, the variability of any single population as measured by their coefficient of variability is about the same, whether upstream or downstream.

Our original model, based on three years of observation, was too simple. We assumed that at the junction of Arrington Creek (where true *Lesquerella lescurii* populations are found only upstream) and the Harpeth River (where true *L. densipila* populations are found only upstream) a large permanent and more or less self-renewing hybrid swarm existed. It was presumed that seeds from the plants of this population were carried downstream, establishing new populations of hybrids. Seeds from these new populations, in turn, were presumed to be carried further downstream, and so on, until they had established a population at the very place where the Harpeth River flows into the much larger Cumberland River. What we had not appreciated fully at the time is the degree of unevenness of the contribution of propagules of the two parental species from year to year. In effect, seeds are dispersed largely as a result of occasional flooding of the rivers and creeks of the area, at which time they overrun their banks picking up seeds at one locality and depositing them at another. As a result of the pattern of highly localized spring storms in the area, the upper Harpeth River and Arrington Creek are likely to carry very uneven

amounts of water. When one of them floods and the other does not, only seeds of *L. lescurii* (from Arrington Creek) or *L. densipila* (from the upper Harpeth) are deposited at the floodplain where these streams meet. When both flood, the hybrid swarm is more intermediate. In 1953 and 1955 the populations close to the junction of the two rivers were fairly intermediate. In 1964 and 1965, on the other hand, they had taken a decidedly *densipila*-like character. However, in 1966, those close to the junction of the upper Harpeth and Arrington Creek were very *lescurii*-like, while those a mile or two downstream were still *densipila*-like. Thus, it appeared that a very recent influx of *lescurii* seeds into the junction hybrid population had taken place.

Populations downstream are somewhat buffered from these effects. Most of the seeds arriving there are probably from hybrid populations upstream rather than from populations of the parental species. Consequently there is less chance for either species to predominate. This is, of course, true the further downstream one goes.

The situation is effectively shown in Fig. 8 where the populations sampled are given by year of collection (1953–1966) and arranged vertically according to a hybrid index of zero to six (see Table 16). Laterally, they are arranged by collection site along the Harpeth River beginning at the point where Arrington Creek enters and extending downstream to the point of its entrance into the Cumberland River.

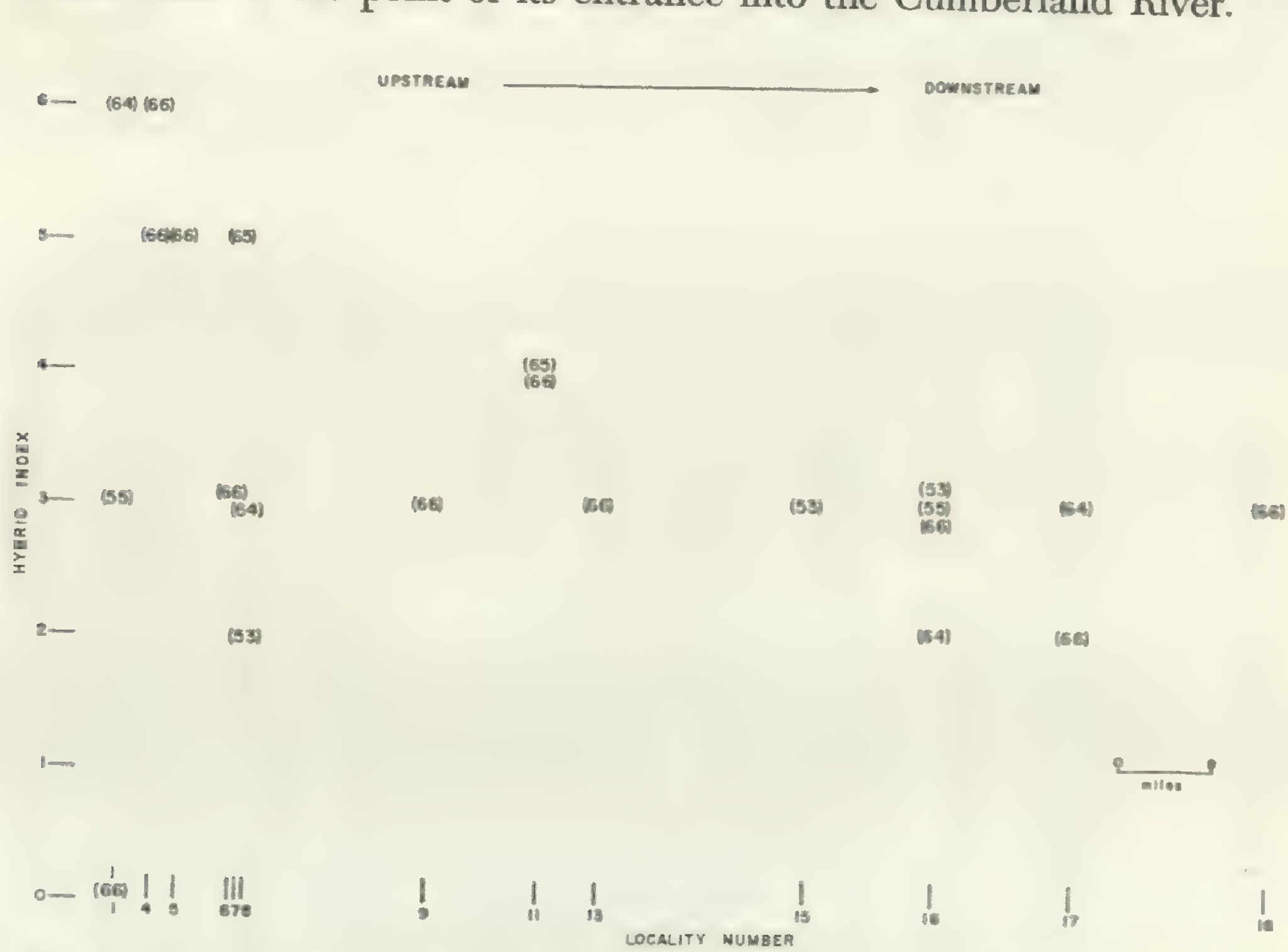

FIG. 8. Chart showing samplings of *Lesquerella densipila* × *L. lescurii* hybrid populations by year of collection (1953–1966) arranged vertically according to their position in a hybrid index from zero (*L. lescurii*) to six (*L. densipila*). Laterally, they are plotted by site position along the Harpeth River from the junction of Arrington Creek at left downstream to its entrance into the Cumberland River on the right at site 18.

TABLE 17. MEAN VALUES FOR CHARACTERS OF FIELD HYBRIDS OF L. DENSIPILA × L. STONENSIS

	Site									
	55–4		61–4		66–4		66–5		66–6	
Character	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
1	—	—	1.51	.59	2.05	1.10	1.62	.96	—	—
2	2.06	.36	1.80	.46	2.39	.41	2.36	.44	2.13	.41
3	4.03	.57	3.72	.65	4.10	.65	4.10	.62	3.41	.49
4	3.72	.42	3.53	.47	3.73	.42	3.78	.44	3.30	.42
5	3.92	.61	3.59	.68	4.64	.53	4.64	.58	3.91	.48
6	0.62	.65	0.63	.75	0.72	.54	0.77	.52	1.02	.54
7	0.22	.41	0.29	.46	0.97	.19	0.94	.24	0.98	.15
8	0.06	.24	0.07	.26	0.89	.31	0.92	.27	0.80	.40
9	0.91	.28	0.93	.26	0.98	.13	0.97	.18	0.98	.15
10	1.00	.00	1.00	.00	1.00	.00	1.00	.00	1.00	.00
11	0.15	.36	0.18	.38	0.06	.24	0.11	.31	0.11	.31
12	1.00	.00	1.00	.00	1.00	.00	0.99	.07	1.00	.00
13	0.00	.00	0.00	.00	0.46	.50	0.36	.48	0.24	.43
14	1.00	.00	1.00	.00	0.65	.48	0.78	.41	0.80	.40
15	0.08	.27	0.00	.00	0.00	.00	0.01	.07	0.00	.00
16	0.24	.43	0.02	.13	0.05	.23	0.21	.41	0.11	.31
17	0.28	.79	0.30	.76	0.08	.36	0.11	.31	0.15	.52
18	1.10	.31	1.16	.37	1.31	.66	1.14	.57	1.18	.53
19	1.04	.20	0.94	.17	1.38	.26	1.31	.26	0.90	.19
20	0.83	.13	1.01	.08	1.01	.26	1.21	.28	1.51	.15
21	0.00	.00	0.00	.00	0.01	.09	0.01	.07	0.00	.00
22	0.69	.47	0.25	.44	0.78	.42	0.73	.45	0.77	.42
23	1.00	.00	1.00	.00	0.22	.42	0.27	.45	0.23	.42

	Site									
	55–1		66–2		55–3		65–3		66–3	
Character	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
1	—	—	2.73	1.26	—	—	1.00	.00	1.62	.65
2	2.20	.42	2.20	.38	2.07	.36	1.94	.45	2.10	.38
3	4.27	.65	3.77	.68	3.94	.57	3.44	.50	3.46	.55
4	3.86	.42	3.26	.38	3.71	.38	3.47	.32	3.29	.42
5	4.83	.57	4.05	.52	4.24	.44	3.59	.47	4.00	.57
6	1.32	.72	0.58	.51	1.01	.76	0.90	.69	0.87	.40
7	0.42	.50	0.26	.44	0.37	.48	0.01	.11	0.93	.25
8	0.07	.25	0.05	.21	0.11	.31	0.02	.16	0.83	.38
9	1.00	.00	0.99	.09	0.94	.25	1.00	.00	1.00	.00
10	1.00	.00	1.00	.00	1.00	.00	1.00	.00	1.00	.00
11	0.00	.00	0.06	.23	0.01	.09	0.15	.36	0.05	.22
12	1.00	.00	1.00	.00	1.00	.00	1.00	.00	1.00	.00
13	0.00	.00	0.00	.00	0.00	.00	0.00	.00	0.00	.00
14	1.00	.00	1.00	.00	1.00	.00	1.00	.00	0.97	.17
15	0.00	.00	0.05	.21	0.01	.09	0.01	.11	0.03	.17
16	0.00	.00	0.35	.48	0.02	.15	0.04	.19	0.20	.40
17	0.00	.00	0.12	.54	0.01	.09	0.16	.46	0.08	.41
18	1.63	.49	1.00	.25	1.19	.45	1.07	.26	1.15	.45
19	1.09	.20	1.05	.20	0.97	.20	1.08	.19	0.88	.20
20	1.05	.18	1.52	.31	1.01	.09	1.01	.16	1.41	.18
21	0.01	.09	0.00	.00	0.00	.00	0.00	.00	0.00	.00
22	0.90	.30	0.51	.50	0.94	.24	0.51	.50	0.47	.50
23	1.00	.00	1.00	.00	1.00	.00	1.00	.00	0.74	.44

TABLE 17. (Continued)

Character	Site 66–7 $\bar{x}$	66–7 s	66–8 $\bar{x}$	66–8 s
1	1.63	1.17	2.14	.83
2	2.37	.40	2.19	.40
3	4.28	.70	3.89	.62
4	3.59	.49	3.53	.44
5	4.32	.57	4.20	.57
6	0.75	.48	0.85	.52
7	0.59	.50	0.95	.22
8	0.28	.45	0.86	.35
9	0.96	.20	0.98	.15
10	1.00	.00	1.00	.00
11	0.04	.20	0.07	.25
12	1.00	.00	0.99	.09
13	0.00	.00	0.43	.50
14	1.00	.00	0.67	.47
15	0.08	.27	0.00	.00
16	0.49	.51	0.21	.41
17	0.08	.44	0.10	.42
18	0.98	.24	1.15	.46
19	1.29	.23	1.14	.20
20	1.24	.24	1.34	.29
21	0.00	.00	0.00	.00
22	0.82	.39	0.65	.48
23	1.00	.00	0.36	.48

At this point there is no evidence to indicate that natural selection is favoring any particular genotype. The observed wide fluctuations appear to be related to catastrophic events (such as the storm pattern and subsequent flooding) rather than to evolutionary forces. However, we are much impressed with the dynamic ebb and flow of the genes of each species into the hybrid populations, and with the wave-like movement of the genetic impact of one species, then the other, on successive hybrid swarms down river from the point where the two species come together.

LESQUERELLA DENSIPILA × L. STONENSIS

When first noticed, this hybrid, on the basis of the species then known, was classified as *Lesquerella densipila* var. *maxima* (Rollins, 1952). However, the particular characters and variability of these populations suggested that they had arisen due to hybridization between *L. densipila* and an unknown species. Later, the putative unknown species was found and given the name *L. stonensis* (Rollins, 1955).

Lesquerella stonensis exists as a pure species at various localities along the East Fork of the Stones River (see Table 12 for localities of seed sources) while *L. densipila* is found as a pure species along the West Fork of the Stones River, as well as to the south and west of this area in the Central Basin (Fig. 1). Both species are found in the flood plains of

the rivers and presumably some of the seed is washed downstream during the annual spring floods. Consequently, where the two forks of the Stones River come together, the two species meet and hybridize and from there to the point where the Stones River flows into the Cumberland, a distance of some 30 miles, only hybrid populations are found (Rollins, 1957). This situation was modified with construction of the J. Percy Priest Dam and Reservoir on the lower part of the Stones River. This reservoir flooded a great many of the hybrid populations and isolated the ones downstream below the dam.

The *Lesquerella densipila* × *L. stonensis* hybrid swarm presents the same basic geographic situation as that of *L. densipila* × *L. lescurii*. The lower Stones River is shorter than the Harpeth, offering less opportunity for differentiation with distance, and the construction of the dam has

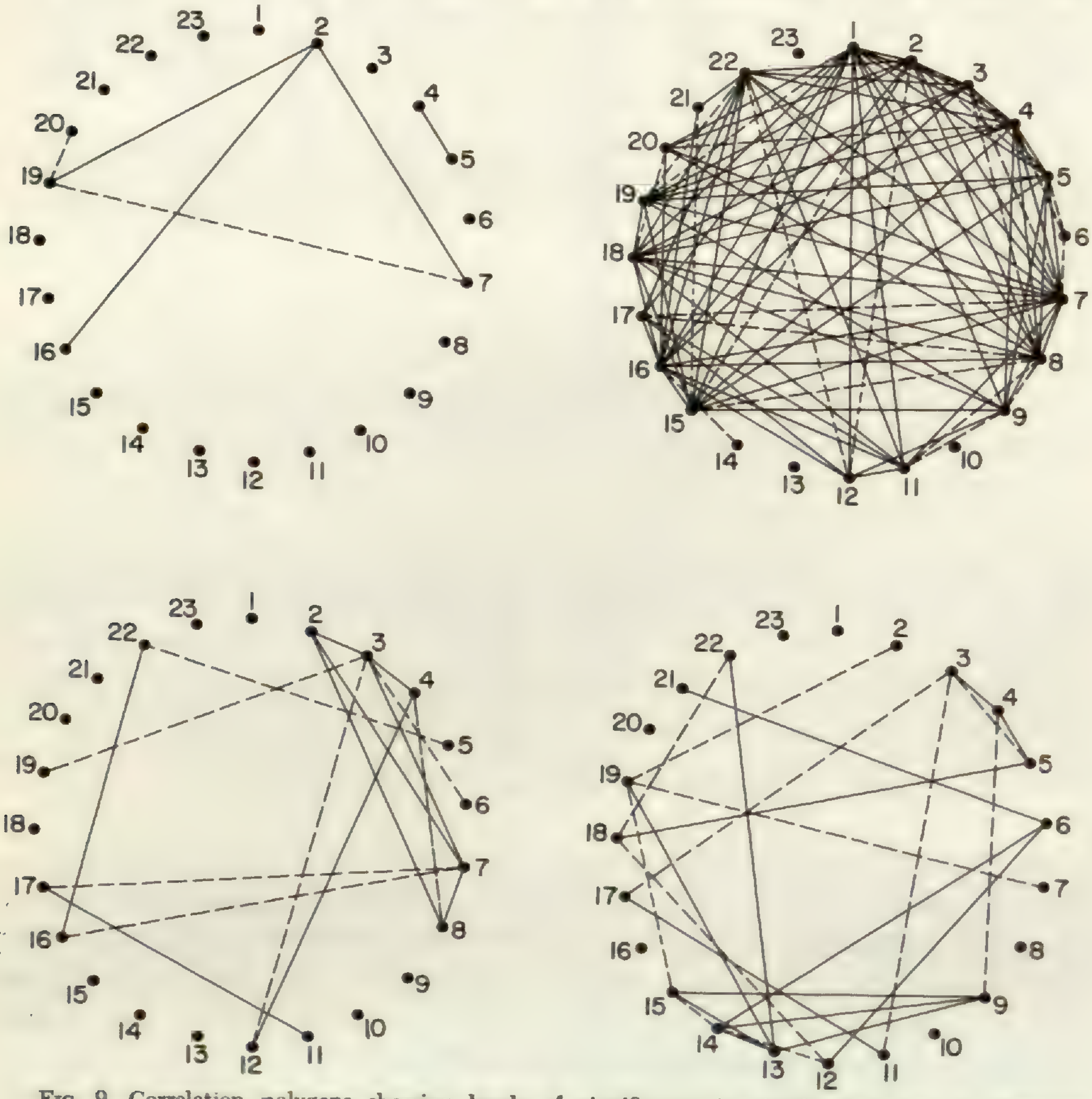

FIG. 9. Correlation polygons showing levels of significance in simple character × character correlation for all 223 possible combinations: full line, correlation significant at the 1% level or better; broken line, correlation significant at the 5% level or better, but less than 1%; no line, correlation significant at a level less than 5%. Upper left, *Lesquerella densipila* (population 66056); upper right, *Lesquerella densipila*, sum of all populations; lower left, *Lesquerella lescurii* (population 66057); lower right, *Lesquerella lescurii* × *L. densipila*, segregating F_2 family from a single parental cross (population 67113).

destroyed any possibility of revisiting many of these populations in the future.

Our account of this hybrid swarm is restricted to a character by character description, mean values for the characters (Table 17), an analysis of the character correlation polygons and a hybrid index (Fig. 9 & 10).

Qualitative Character by Character Description

Flower color (Character No. 1). *Lesquerella densipila* has yellow flowers while *L. stonensis* has white flowers. On a scale of 1 to 5 (with 1=white) the hybrids tend to be intermediate or toward the white parent and no significant difference is found between the various populations (Fig. 11). The natural hybrids are more frequently white in color than the artificial hybrids.

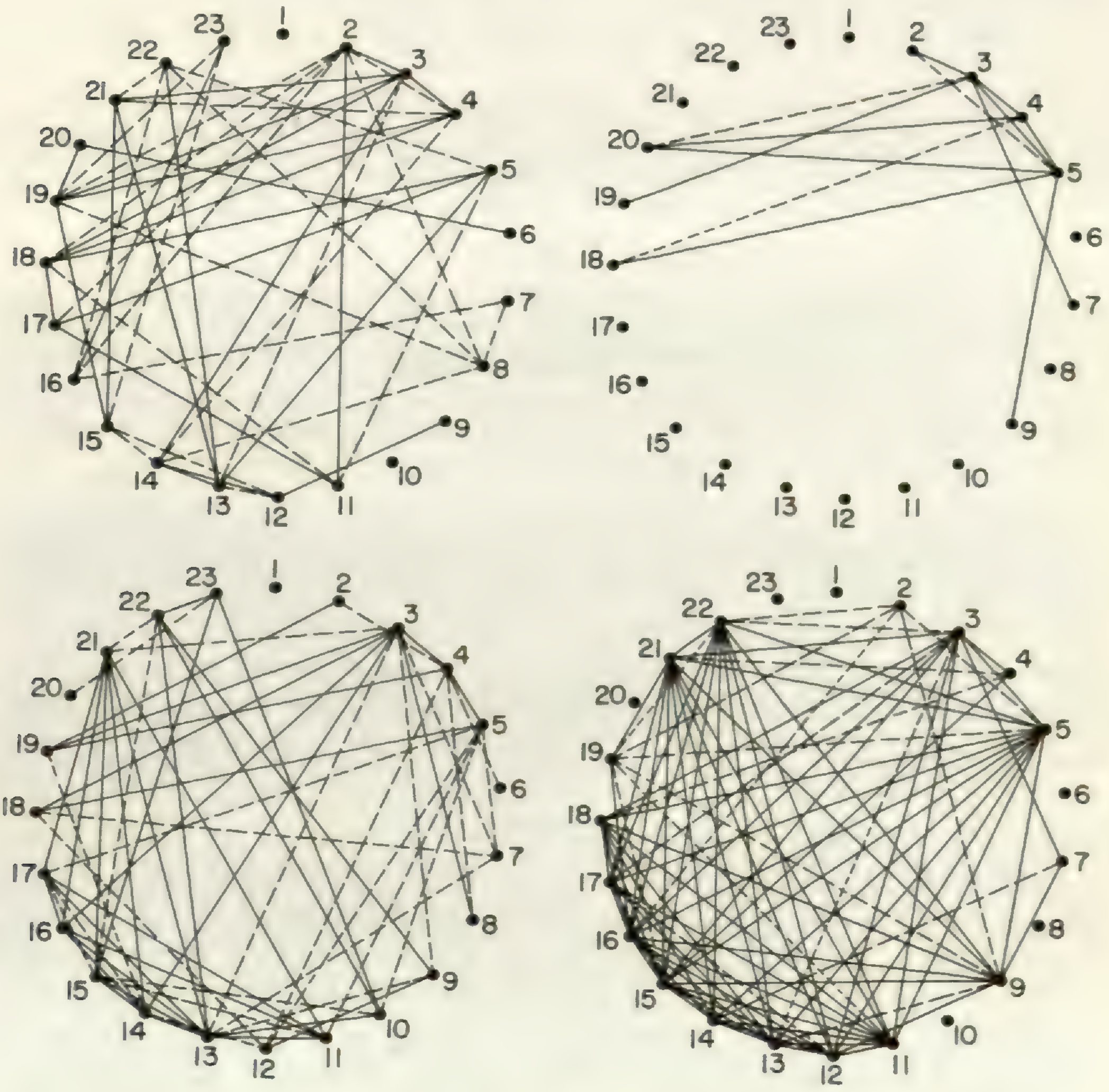

FIG. 10. Same as figure 9. Upper left, *Lesquerella densipila* × *L. lescurii*, natural hybrid population from site 18 (66070); upper right, *Lesquerella densipila* × *L. lescurii*, natural hybrid population from site 1 (64074); lower left, *Lesquerella densipila* × *L. lescurii*, natural hybrid population from site 17 (64073); lower right, *Lesquerella densipila* × *L. lescurii*, natural hybrid population from site 1 (55115).

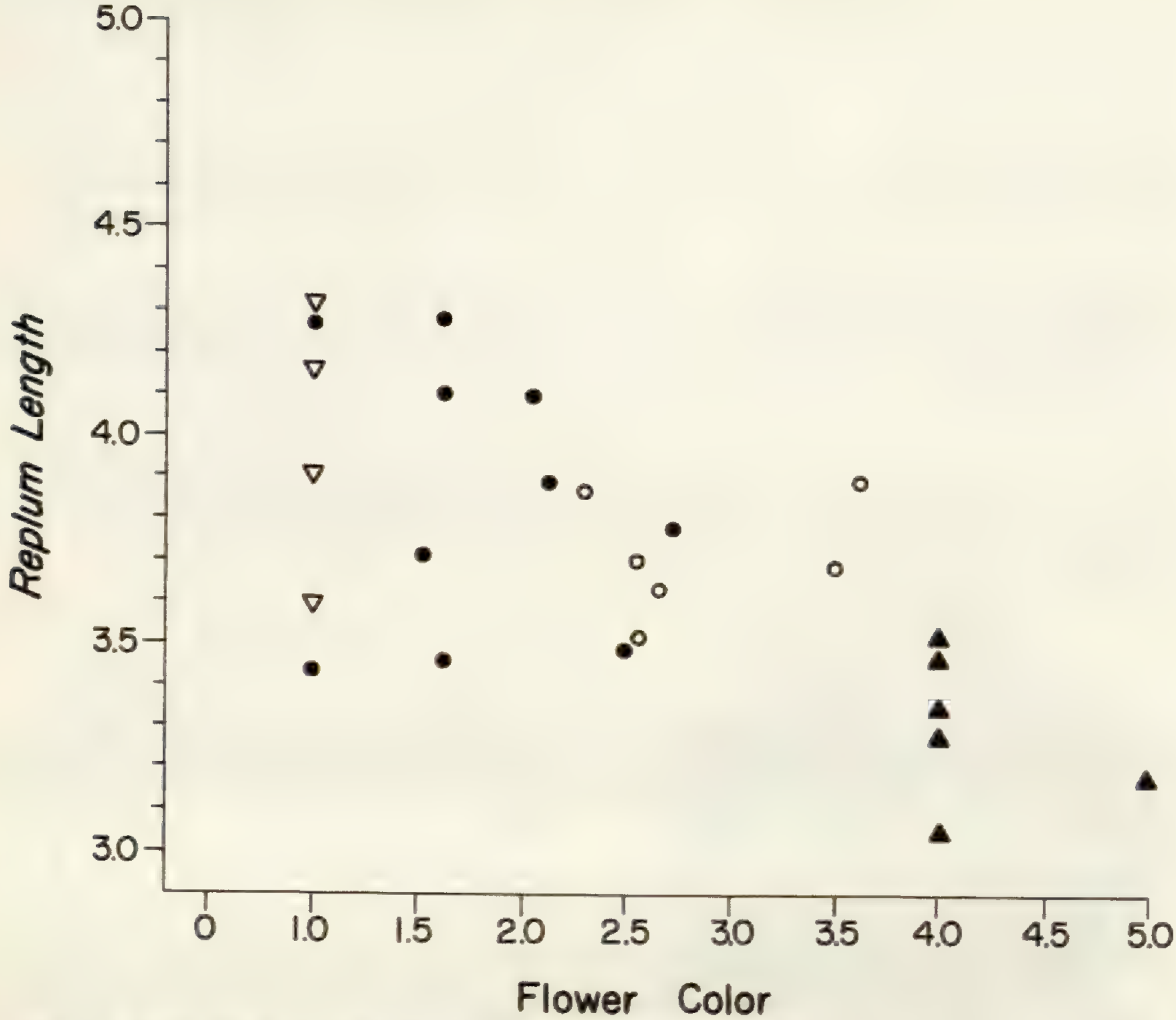

FIG. 11. Mean replum length (mm.) vs. flower color (1=white, 5=yellow) in populations of *Lesquerella*. Open triangles: *L. stonensis*. Solid triangles: *L. densipila*. Solid circles: *L. densipila* × *L. stonensis*, field populations. Open circles: *L. densipila* × *L. stonensis*, garden populations.

Style length (Character No. 2). Populations of *Lesquerella stonensis* have longer styles ($\bar{x}$=2.1 to 2.4 mm.) than *L. densipila* ($\bar{x}$=1.6 to 1.9 mm.). The artificial hybrid population as a whole had an overall mean for this character of 2.06 with some families with a value as low as 1.87 and as high as 2.14. The natural field hybrids showed higher values. The lower value was in population 61–4 ($\bar{x}$=1.80), the highest in population 66–4 ($\bar{x}$=2.39), with most populations having values between 2.1 and 2.3, well within the range of the *L. stonensis* parent (Fig. 12).

Replum length (Character No. 3). *Lesquerella stonensis* has a slightly longer replum than *L. densipila* (3.6 to 4.3 mm. to 3.0 to 3.5 mm. for *L. densipila*). The artificial hybrids are intermediate with a grand mean value of 3.7 mm. Natural field hybrids are varied, but approximate the *L. stonensis* parent more than that of *L. densipila* ($\bar{x}$=3.44 to 4.28 mm.). No geographical or temporal trend could be observed (Fig. 13). The standard deviation and coefficient of variation for all populations was similar.

Replum width (Character No. 4). The replum is wider in *Lesquerella stonensis* ($\bar{x}$=3.7) than in *L. densipila* ($\bar{x}$=3.3). In the artificial hybrids the

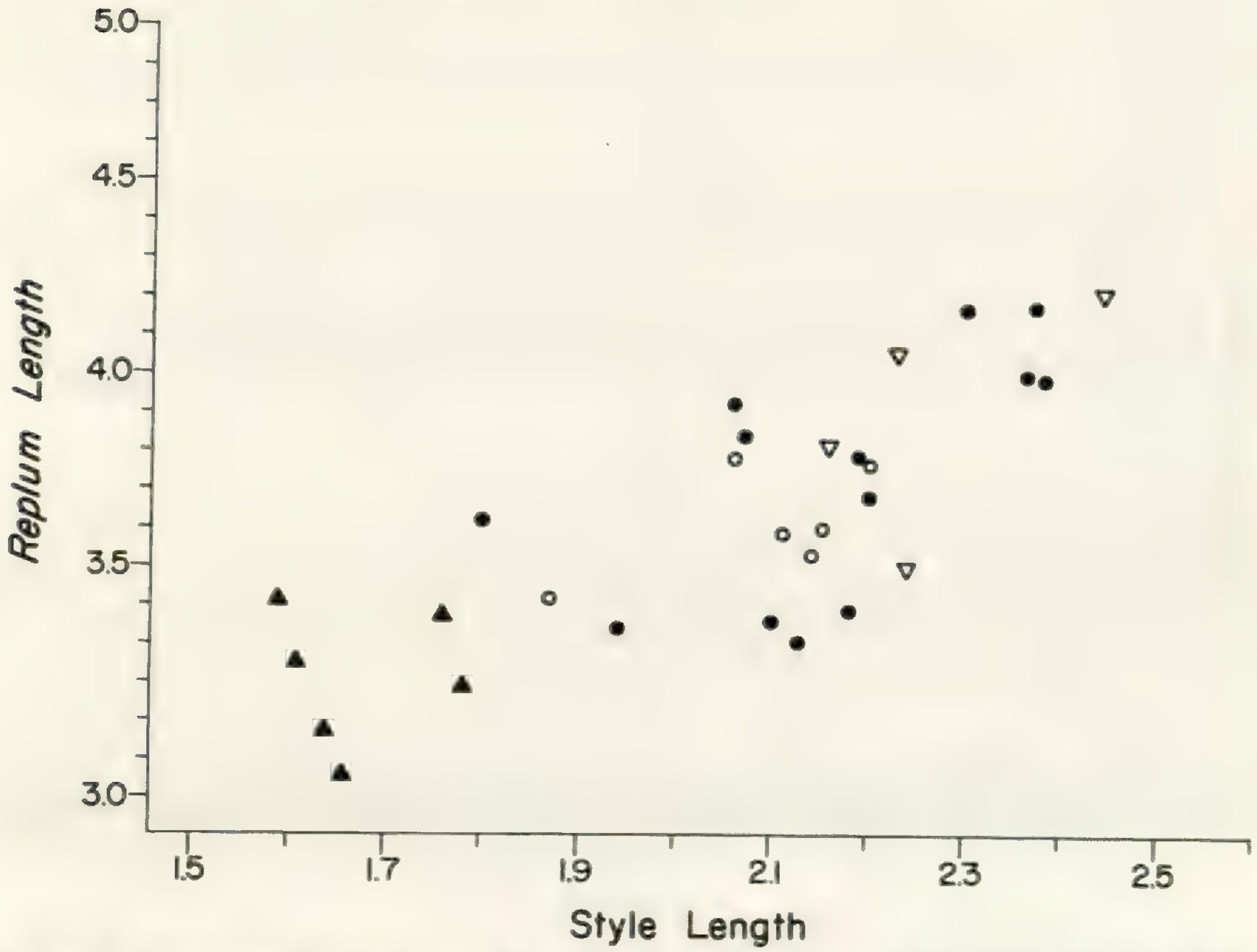

FIG. 12. Mean replum length (mm.) vs. mean style length (mm.) in populations of *Lesquerella*. Solid triangles: *L. densipila*. Open triangles: *L. stonensis*. Solid circles: *L. densipila* × *L. stonensis*, field populations. Open circles: *L. densipila* × *L. stonensis*, garden populations.

replum is slightly narrower than in either parent ($\bar{x}$=3.2), while in the natural hybrids it is very variable, in some populations being as narrow as the artificial hybrid ($\bar{x}$=3.26) and in others as wide or wider than *L. stonensis* ($\bar{x}$=3.86). The coefficient of variation in each population is on the order of 10% which is lower than for some of the other characters. Why this character is so variable from population to population, but so relatively uniform within each population, is not known to us.

Silique width (Character No. 5). This is a good character to separate the two species, the siliques of *Lesquerella stonensis* being much wider ($\bar{x}$=4.4 mm.) than those of *L. densipila* ($\bar{x}$=3.51 mm.). Artificial hybrids are intermediate ($\bar{x}$=3.9 mm.) although there is some variation from one genetic family to another (range from 3.6 to 4.2 mm., Fig. 14). Natural hybrid populations tended to be intermediate or closer to the *L. stonensis* parent ($\bar{x}$=3.92 to 4.62) although two populations had values reminiscent of *L. densipila* ($\bar{x}$=3.89) and three had values well within the range of *L. stonensis* ($\bar{x}$=4.64, 4.64 and 4.83). The coefficient of variation ranged from 11% to 19%.

Septum perforation (Character No. 6). *Lesquerella stonensis* has a small perforation in the center of the septum that occupies about a third of the total septum area, while *L. densipila* has unperforated septa. Artificial hybrids tend to have very small perforations in their septa, as do

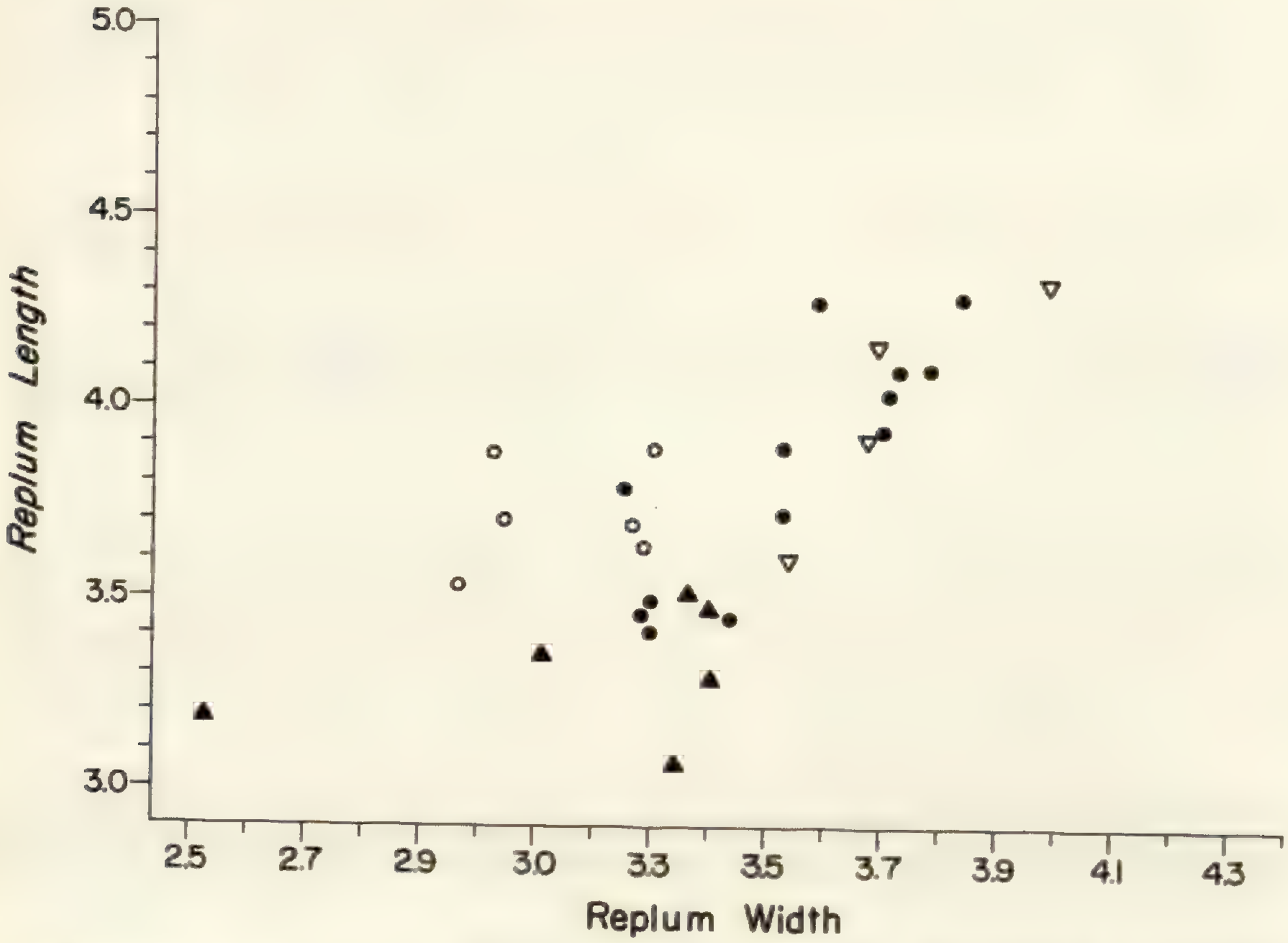

FIG. 13. Mean replum length (mm.) vs. mean replum width (mm.) in populations of *Lesquerella*. Solid triangles: *L. densipila*. Open triangles: *L. stonensis*. Solid circles: *L. densipila* × *L. stonensis*, field populations. Open circles: *L. densipila* × *L. stonensis*, garden populations.

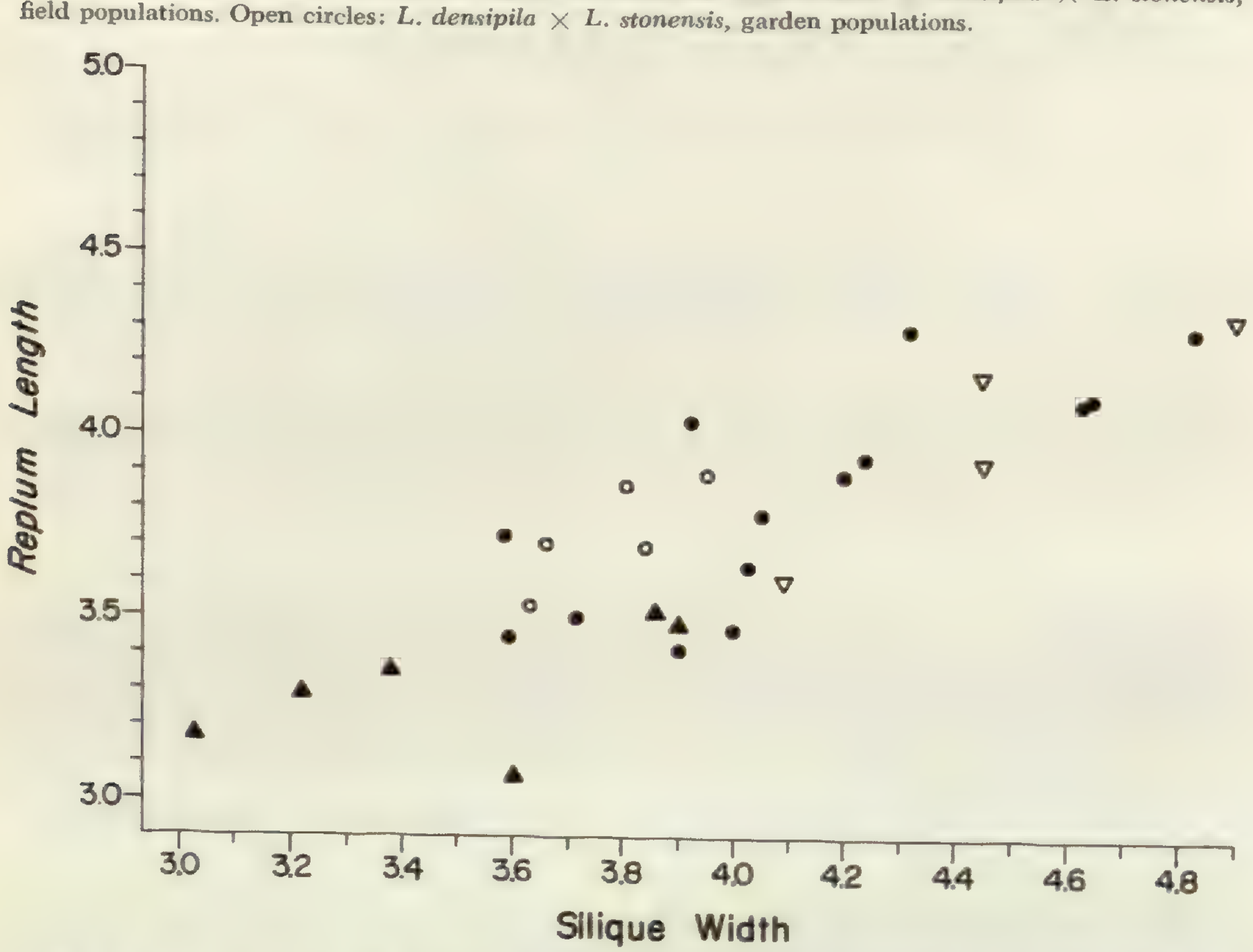

FIG. 14. Mean replum length (mm.) vs. mean silique width in populations of *Lesquerella*. Solid triangles: *L. densipila*. Open triangles: *L. stonensis*. Solid circles: *L. densipila* × *L. stonensis*, field populations. Open circles: *L. densipila* × *L. stonensis*, garden populations.

natural hybrids. A great deal of variation in this character exists in the population, however, and some hybrid plants have no perforation, while others have a perforation as large as that of *L. stonensis*. The size of the perforation is less of an indicator of hybridity in the population than the fact that the population segregates for this character. This points to a rather simple genetic base for the character, whose adaptive significance is hard to conceive. As for variation from population to population, it is not significant and no geographical or temporal trend was observed.

Replum apex (Character No. 7). In *Lesquerella densipila* the replum apex is rounded (Fig. 2) and is scored as 0 while in *L. stonensis* the apex tends to be anguar and is scored 1. Scoring each plant as 1 or 0, approximately 60% of all plants of *L. stonensis* are found to have pointed apices ($\bar{x}$=0.56). The artificial hybrid populations are intermediate with an average index value of 0.23. Natural hybrid populations are tremendously variable for this character. One population has essentially all plants with rounded apices (index value .01) while 5 of the twelve populations have practically all plants with pointed apices (index values 0.93–0.98). Two populations have an index value similar to the *L. stonensis* parent (0.42 and 0.59) while the other four populations have values similar to the artificial hybrids (0.29–0.22). Most populations either resemble the *L. stonensis* parent or transcend it in the pointedness of the replum. It is hard for us to see any selective reason for this pattern of variation, particularly in view of the fact that no geographical trend is apparent. A similar lack of pattern was observed for this character in the hybrids between *L. lescurii* and *L. densipila*, where we concluded that there probably was a large environmental component influencing the expression of this character, and that it was a poor indicator of hybridity. The same appears to be true here.

Replum base (Character No. 8). What has been said of the replum apex applies as well to the base. Furthermore there is no substantial difference between the parent species populations in this character.

Trichomes at the base of the style (Character No. 9). Both species, and consequently their artificial and natural hybrids as well, have trichomes at the base of the style.

Trichomes on the outer surface of the valve (Character No. 10). Both species have trichomes on the outer surface of the valve and so do the hybrids.

Trichomes on inner surface of the valve (Character No. 11). Neither of the species ordinarily have trichomes on the inner surface of the valve nor do the artificial hybrids. However, between one and 18 per cent of the natural hybrid populations have plants with at least some trichomes on the inner surface. Two of the populations of *Lesquerella densipila* studied had up to 4 per cent of their plants with some trichomes on the inner surface. That the genetic potential for trichomes on the valve interior is present in *Lesquerella* is shown by the fact that it occurs consistently in

L. lescurii. However, we do not know the exact source in the case of these hybrid populations.

Trichomes on replum (Character No. 12). Both species have trichomes on the replum and so do all the hybrids.

Silique apex (Character No. 18). Both species have rounded or slightly depressed apices. Those of *Lesquerella stonensis* are somewhat more depressed than those of *L. densipila*. Both the artificial and the natural hybrids tend to have apices slightly more pointed than their parents. In general, the populations are quite uniform for this character.

Infructescence (Character No. 19, 20). The infructescence of *Lesquerella densipila* is more compact with shorter pedicels that are closer together than those of *L. stonensis*. The artificial hybrids resemble *L. densipila* both in pedicel length and in the number of pedicels per linear centimeter of infructescence. The artificial hybrids are slightly more intermediate, particularly in the length of the pedicels. It is possible that the more compact infructescences of the hybrids than expected is due to slower growth of the hybrids.

Summary of character by character variation. *Lesquerella densipila* resembles *L. stonensis* more than it does *L. lescurii* and consequently there are only a few characters that discriminate *L. densipila* and *L. stonensis*. Other than flower color, they are mostly quantitative characters. The only pattern observed in the populations of natural hybrids is a tendency of many of them to resemble *L. stonensis* more than *L. densipila*. This is presumed to be due to an uneven overall contribution of the two species to the hybrid swarms. Circumstantial evidence suggests that *L. stonensis* was present along the Stones River in pure form before *L. densipila* entered. The natural hybrid populations studied appeared not to have become fully intermediate between the two species because of a predominance of *L. stonensis* in the valleys of the river system. No differences between upstream and downstream populations were observed.

Correlation coefficients. Analysis of the correlation polygons of the *Lesquerella densipila* × *L. stonensis* hybrid populations reveals the following:

1) no population shows high levels of correlation;

2) in several populations the character by character correlation is almost negligible;

3) no geographical trend is visible.

In our opinion these results reflect (1) the greater genetic similarity of *Lesquerella densipila* with *L. stonensis* when compared with the genetic similarity of *L. densipila* and *L. lescurii*, and (2) the lack of the geographical mixing effect observed in the *L. densipila* × *L. lescurii* hybrids. In this respect it reinforces the results obtained from the morphological analysis.

Hybrid index. A simple hybrid index was constructed and populations scored accordingly (Table 18). It confirmed what the analysis of characters had already shown, namely, that the hybrid populations are either

TABLE 18. HYBRID INDEX NUMBERS FOR CHARACTERS IN WILD POPULATIONS OF L. DENSIPILA × L. STONENSIS

Pop. site	Character Number* 1	2	3	4	5	6	7	8	22	Total
55–1	0.50	0.00	0.00	0.00	0.00	0.25	0.25	0.00	0.00	1.00
66–2	0.50	0.00	0.25	0.75	0.50	0.50	1.00	0.00	0.50	4.00
55–3	0.50	0.50	0.00	0.00	0.25	0.50	0.50	0.00	0.00	2.25
65–3	0.00	0.50	1.00	0.50	1.00	0.50	1.00	0.00	0.50	5.00
66–3	0.25	0.25	1.00	0.75	0.50	0.50	0.00	1.00	0.50	4.75
55–4	0.50	0.50	0.00	0.00	0.50	0.50	1.00	0.00	0.50	3.50
61–4	0.25	0.75	0.25	0.50	1.00	0.50	1.00	0.00	0.75	5.00
66–4	0.50	0.00	0.00	0.00	0.00	0.50	0.00	1.00	0.25	2.25
66–5	0.25	0.00	0.00	0.00	0.00	0.50	0.00	1.00	0.25	2.00
66–6	0.50	0.25	1.00	0.50	0.50	0.50	0.00	1.00	0.25	4.50
66–7	0.25	0.00	0.00	0.50	0.25	0.50	0.00	1.00	0.25	2.75
66–8	0.50	0.25	0.00	0.50	0.25	0.50	0.00	1.00	0.50	3.50

L. densipila=1
L. stonensis=0
*For character number code see Table 1.

intermediate or they tend to resemble *Lesquerella stonensis* more than *L. densipila*. The only exception was population 55–1 from near the junction of the East Fork and West Fork of Stones River which was quite similar to pure *L. stonensis*. The index also confirmed that there is no detectable geographical pattern, or for that matter, any pattern from year to year.

LESQUERELLA DENSIPILA × L. STONENSIS—SUMMARY

The pattern of variation of the populations of this hybrid is more in keeping with the classical model of hybridization. The populations are either intermediate or they show a greater resemblance to one parent than the other, due presumably to backcrossing and introgression. From our experience with these particular populations, we cannot add anything of significance to the well-known model of interspecific hybridization.

Genetic Coherence

Segregations within hybrids between contrasting ecotypes of the diploid species *Potentilla glandulosa* (Clausen and Hiesey, 1958; 1960; Clausen, 1967) indicate that the traits distinguishing ecotypes are regulated by small systems of genes that have additive, inhibitory, complementary and epistatic effects. The individual genes that govern each character are not assembled on one or two chromosomes, but are distributed among several, if not all the chromosomes of the genome. Consequently, each chromosome carries genes that contribute to the phenotypic expression of several characters (Clausen, 1967). This phenomenon, observed by Anderson (1949) before and called the "recombination spindle" by him, provides a system of hereditary components interlocking into a kind of coherence.

Genetic coherence is a mechanism that favors the resegregation of the parental genotypes, with a greater frequency than would be expected if free recombination were operable. According to Clausen, it represents a cohesive force in evolution. The method employed for measuring genetic

coherence is to determine the nature of the correlation of pairs of segregating parental characters as compared with free Mendelian recombination. However, this measure requires an extended analysis. Statistically, measures of correlation and a test of their significance demonstrate only that two variates of a given sample vary or not in such a way as to maintain a definite relation to each other. They tell nothing about the cause of the relationship. Assuming a correlation between two varieties (even when statistically significant) to indicate a relationship between the variates is a most common fallacy. Correlation by itself, then, is not a demonstration of genetic coherence.

Another point worth emphasizing is that the coefficient of correlation r is dependent upon the magnitude of the difference between the means $\bar{x}$ and $\bar{y}$, as well as the deviations of the x_i and y_i from the means. Consequently, if the mean of two characters differs by, let us say, only 0.1 mm., even if the two variables measured are completely independent variables, measure of r will be smaller and possibly less significant statistically than a case where the means $\bar{x}$ and $\bar{y}$ differ by let us say 100 mm., and the two variables $\bar{x}$ and $\bar{y}$ are only partially correlated. This presents an added problem when using the correlation coefficient to measure genetic cohesion.

On the other hand, if genetic coherence exists, certain predictions can be made: (1) since coherence is a phenomenon that tends to keep the genotype intact in a segregating hybrid population, it should not be expressed in a stable, non-hybrid population where presumably the genome is working harmoniously. Therefore, no correlation should be detected in such a situation, and any correlation found in the parental population should be attributed to other causes. Furthermore, cohesion should be strongest in an F_2 hybrid population and weakest in a stabilized hybrid population.

Analysis of the correlation polygons indicates the following:

1) The parental populations show few correlations.

2) The artificial F_2 hybrid populations when taken as a group show a very high degree of correlation.

3) The individual F_2 families do not show as strong a correlation as the lumped F_2. This is perhaps due to the smaller size of the sample, but possibly it represents a sample error in that only the offspring of one particular F_1 cross is being analyzed.

4) The field situation is more involved, but in general it indicates the following: (a) populations that resemble strongly one of the parents show a small degree of correlation; (b) populations that are hybrid intermediates show more correlations; (c) populations suspected of being "primary" hybrids (64–1, 55–1) show the strongest correlation of all.

The results confirm the proposition that genetic coherence exists and is not just the result of statistical manipulation. It also confirms the idea that coherence acts as a conservative force in evolution that tends to slow down recombination.

On the other hand, an interesting phenomenon has been detected. Certain of the hybrid populations of *Lesquerella densipila* × *L. lescurii* morphologically intermediate or slightly similar to *L. lescurii* no longer show genetic coherence, and characters recombine independently. Presumably, in these populations recombination has proceeded over a sufficient number of generations so that the original parental chromosomes have been broken up by crossing-over, and most linkage combinations between *L. lescurii* and *L. densipila* genes are present in the population. Such a population presumably has now acquired unique linkage combinations and if crossed to either parent would show genetic coherence in favor of the hybrid combinations. Such may be the beginning of the process of hybrid stabilization, which would afford a certain amount of protection against occasional gene flow, particularly if lethal or semi-lethal genes were to accumulate in the population.

SUMMARY AND CONCLUSIONS

The detailed analyses of the two hybrid swarms presented above reveal an involved pattern of variation. The original model postulated that at the junction of the streams (Arrington and upper Harpeth in the case of the *Lesquerella densipila* × *L. lescurii* hybrids, and West and East forks of the Stones River in the case of the *L. stonensis* × *L. densipila* hybrid) a hybrid swarm was formed. It was further postulated that seeds of these F_1 and F_2 hybrids were carried downstream by the river during spring floods and deposited at near localities below, where hybrid populations arose. Seeds of these hybrid swarms were deposited at new localities below in subsequent years, and so on. If this were the case, the hybrid material formed at the upper reaches of the river would move down river stepping-stone fashion and presumably natural selection would be acting on the hybrid populations all the time. One reason the present study was undertaken was to determine whether the original model was adequate, and to ascertain the course of change of the hybrid swarm if some effects of natural selection could be shown to be taking place.

Our study has shown that the original model was incomplete and to some degree misleading. What we did not fully appreciate earlier was the fortuitousness of the input of propagules from each of the parental species. Rather than a true mixing of the genotypes of the two species where the rivers meet, with selection working on the hybrid swarm to narrow the variation, the two genotypes hybridize gradually down the river so that it is only fairly far downstream that intermediate hybrid swarms are found. The uneven seed contribution of each species from year to year is related to local conditions. In most years, one or the other of the upper tributaries of the main stream floods, bringing with it seeds of the pure species that grows near the river. These seeds are not only deposited at the junction of the two rivers but in diminishing amounts at localities down river from the junction. The following year seedlings of that species may germinate at these sites, together with seedlings of the

other species and of hybrids that grew there before. Hybridization takes place, but since the number of seedlings of one of the species may be more abundant than that of the other, the resulting hybrid swarm is not truly intermediate. In the following year, the same pattern of flooding might take place so that more seeds of the same species are deposited, or it might be reversed, and the locality is flooded with seeds of the second species. The result is either a more or less intermediate hybrid swarm, or more likely one that is strongly influenced by one or the other species.

Seeds from these upstream hybrid populations are carried by the river during spring flooding to localities further downstream. Here they germinate and cross with the hybrids that are present there. The arriving seed will be more like one parent some years, more like the other in other years. The resulting hybrids will be more intermediate than the arriving seed. Consequently the further downstream the more intermediate the hybrid populations become until true intermediacy is achieved.

We cannot emphasize too strongly the fact that a very dynamic situation obtains along the Harpeth River. Not only are the hybrid populations subjected to the effects of new inputs of seeds of a diverse nature from upstream, but the sites where they grow are being changed from one kind of agronomic practice to another. Different crops are planted in different years or the land is shifted from cultivation to grazing, etc. Such changes can be a large factor in expanding or contracting or even obliterating a population on a given site.

Some of the significance of the hybrid picture of the Lesquerellas of the Central Basin relates to the overall role hybridization has played in the origin and differentiation of plant species. It is easy to visualize similar patterns having occurred repeatedly over geological time. The movement of the hybrids away from the parental species provides the mechanism which would enable a new taxon different from either of the progenitor species to originate.

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THE USE OF ELECTRONIC DATA PROCESSING METHODS IN THE FLORA OF VERACRUZ PROGRAM[1]

ARTURO GÓMEZ-POMPA
AND
LORIN I. NEVLING, JR.

We are living and working in a period when floristic studies far exceed any similar emphasis of the past. They comprise a very significant portion of the systematic studies now underway and appear to be steadily increasing. Even a decade ago floristic studies were not fashionable and, in fact, received considerable criticism from many quarters. It is not intended to imply here that floristics are fashionable today. However, the realization that man is destroying the world before he has taken the opportunity to know and understand the diversity of plants occurring on the earth's surface has had a profound influence on the thinking of many systematic botanists. Many systematists feel a strong moral obligation to document this diversity as best they can before it is too late, and find that floristics offers the most expeditious way to do so. The production of a flora for a given geographical area is a much more difficult task today than it was even a few decades ago. The pressure of time has been mentioned but several additional factors contribute their burdens. Among these is our steadily increasing knowledge of the processes of organic evolution that have to be dealt with and the desire, if indeed not necessity, of understanding the "biology" of the plant groups under study. Also, there are new and urgent demands for increased accuracy of all the data included in the ultimate treatment.

Scientific knowledge grows unevenly and at some point it is most helpful to have this brought together in a synthesized[2] form. A flora can be the vehicle to accomplish this. It should not only be a work of synthesis, which is in itself an accomplishment, but it should also help spawn new and original research. In this way, a floristic study can help to build a new plateau of knowledge upon which other researchers can enlarge. Floras should never be considered as the end point of concern with the plants of a given region but as the beginning.

STEPS IN THE PREPARATION OF A FLORA

During the initial consideration of the Flora of Veracruz, we made a

[1]Flora of Veracruz. Contribution No. 10. A joint project of the Instituto de Biología, Universidad Nacional Autónoma de México and the Arnold Arboretum and Gray Herbarium of Harvard University. (See An. Inst. Biol. Univ. Nal. Autón. México, Ser. Bot. 41: 1, 2. 1971). This study was partially supported by grant GB–20267X from the National Science Foundation to the junior author.

The authors wish to express their appreciation to numerous colleagues, both here and in Mexico, for helpful suggestions, corrections, and criticisms of this manuscript.

[2]Synthesized is used here in the sense of including original data gathering in addition to summarizing previously known information.

general analysis of the usual steps in the preparation of a flora. The basic data and procedures employed seem to vary somewhat from one project to another, just as content and quality vary. In spite of this, most floristic studies do share some common data sources, procedures and problems, each of which is discussed briefly as background information.

Ideally, the ultimate flora would contain all the information known for each taxon regardless of the subject. At the present time, there are serious obstacles to this, one of which is gaining easy access to diverse bibliographic data sources. There are, of course, other problems inherent in gathering data to be used in a flora. Otherwise one might expect that most of the flora of the world would have been covered by this time. The bibliographic problem manifests itself in several ways. All floras begin with some kind of basic bibliography which probably will be most useful at the beginning of the study of a group and again toward the end. These two "peaks" of usage serve somewhat different functions. The first involves an initial search for papers dealing with taxonomy, nomenclature, distribution, etc. These papers, along with specimens, form the basic building block for the development of plant descriptions and keys. The second bibliographic "peak" is usually reached as the rough framework of taxonomic structure has been completed. The usage here tends to be more specialized as the topics tend to be more specialized; for example, the search may be for detailed environmental data, ecology, chemical compounds, etc. One problem inherent in the bibliographic process is relatively simple in theory and difficult in practice: to generate a more or less complete bibliography. The second part of this problem, i.e., the specialized reference, is more complex because considerable *individual* judgment must come into play as to whether to include a paper or not.

The reliability of published information always must be assessed. It is often difficult to determine which taxon the data should be assigned to; for example, many ecological and some phytochemical studies are not backed by voucher specimens. This is also the case with the earlier works in cytology and anatomy. A degree of uncertainty should be anticipated in all descriptive material whether vouchered or not. The ultimate responsibility for proper assessment lies with the individual worker.

Another bibliographic problem concerns the extent to which references are cited in the published flora. The citation of bibliographic references might be considered a part of the description—those dealing with nomenclature certainly are—but many floras have chosen to treat the remainder in a separate category. It is our impression that bibliographic references add significantly to a flora because they furnish the user with a baseline of information to interpret the floristic treatment. Furthermore, we feel that often there is a definite correlation between the number of references cited and the final quality of the work. One should be selective in this matter, however, and not include a reference solely because a particular species is mentioned. It is not especially helpful to have a bibliography

more extensive than the text. In the final analysis, the most difficult problem involving bibliographic resources is to maintain them in such a way as to keep them accessible. This task is compounded as the amount and diversity of information increases and it can be the main reason for not including information that is important.

We doubt that it is necessary to direct much attention to the methods of obtaining original data resources, that is, living plants and herbarium specimens, as most of us are familiar with this aspect of systematic research. Suffice it to say that it is necessary to have a collection of specimens which is representative of the morphological variation and geographic distribution of the taxa.

The combination of the two basic resources, bibliography and specimens, leads to the common procedure of preparing keys and descriptions of taxa (admittedly the content varies considerably from flora to flora). In most, however, the description constitutes the main mode of data presentation and accordingly forms the body of the flora. Descriptions of each species consist of some or all of the following categories: the scientific name and some or all of its synonyms, including typification; a morphological description based on data from literature and specimens; diverse data such as chromosome number, phenology, chemical compounds, uses, local name; ecology; illustrations; geographic distribution in the area and in a broader perspective, sometimes with maps. When specimen citations are included they most commonly consist of the collector's name, number, and the locality. In more comprehensive floras, herbarium abbreviations may be included as well. In our opinion, specimen citations add greatly to the usefulness of any flora but most particularly to those of tropical areas.

It is the usual practice to develop generic descriptions from the species treated, unless the generic descriptions are meant to be worldwide in circumscription. Family descriptions are generated in a like manner from generic descriptions. Uniformity of descriptions, even within a single flora where a certain amount of format change may occur, is difficult to obtain. Often this means that descriptions are difficult to compare.

The preparation of keys to all taxa is of prime importance. The keys are necessary to provide access to the proper data (description). Often the keys are the most used part of a flora and they should be constructed with the greatest care and with their frequency of use firmly in mind. Keys are one of the most variable portions of a flora because different criteria may be used for different families; for example, keys based on fruit, flower, leaves, or pollen may have a different diagnostic usefulness in different genera and families, and consequently some are stressed (weighted) while others are not. The most reliable and easily used characteristics should be chosen for the keys.

A related problem is that of compatibility with other floras, i.e., whether they can be used in conjunction with one another without serious data conflict. Frequently a flora of a particular region becomes the base for a

flora either of a smaller area that is a portion of it, or a larger region that includes it. Even though there is a general awareness of this, it is a rare flora that has been planned for such contingencies. The greater the amount of data included in a given flora, the greater the probability that a useful data base will be established.

Finally, the most frustrating procedures in flora preparation are those belonging to all the categories mentioned above, which might be thought of as being routine. Some examples of routine operations are: preparing duplicate labels for recently collected specimens; bibliographic search, particularly in peripheral areas such as the environmental aspects of the area; determination of localities for mapping purposes; and the elaboration of specialized catalogues, such as local names.

In recent years several attempts have been made to solve some of the problems mentioned, with varying degrees of success, by using automatic data processing techniques. After an examination of these efforts, we came to the conclusion that they offered great possibilities, not fully explored, to free the professional botanist from many routine operations. The possibility of increased efficiency, without greatly increased costs, appeared to be a realistic and attainable goal. Several methods were explored before a practical system for the Flora of Veracruz was developed.

The decision to use electronic data processing methods for our flora was made in 1966, when the first pilot projects were completed. These included information retrieval of herbarium specimen data and automatic map production for range distribution. The results of these pilot projects were presented at our Mexico City Symposium on Information Problems in Natural Sciences in 1967 (Gómez-Pompa & Olvera, 1967; Scheinvar, Gómez-Pompa & Alonso, 1967). It is worth mentioning that during the initial developmental stages of our work other floristic projects were stimulated by our approach, results, and personnel (Ahumada, 1967). We are encouraged that in these few years the quality and number of other floristic programs using electronic data processing methods have increased considerably. The approaches for different applications have also increased and diversified (Morse, 1971; Bestchell & Soper, 1970; Scheinvar & Gómez-Pompa, 1969; Crovello & MacDonald, 1970). It is important to realize that many of these techniques were inspired by the pioneer work of Perring (1963) and Soper (1964), which are, to our knowledge the first large scale attempts to use EDP methods for specific floristic projects. Rogers' work on Information Retrieval for Taxonomy (1960) should be mentioned here, even though not floristic in its approach, as it presents many of the basic ideas used for EDP-IR application to floristic studies. It is also worth mentioning the effort of the Smithsonian Institution in this field (Squires, 1966).

Data Processing for the Flora of Veracruz

The possibilities of the kinds and amount of data to be provided in a floristic work are endless and may range from the collection number of a

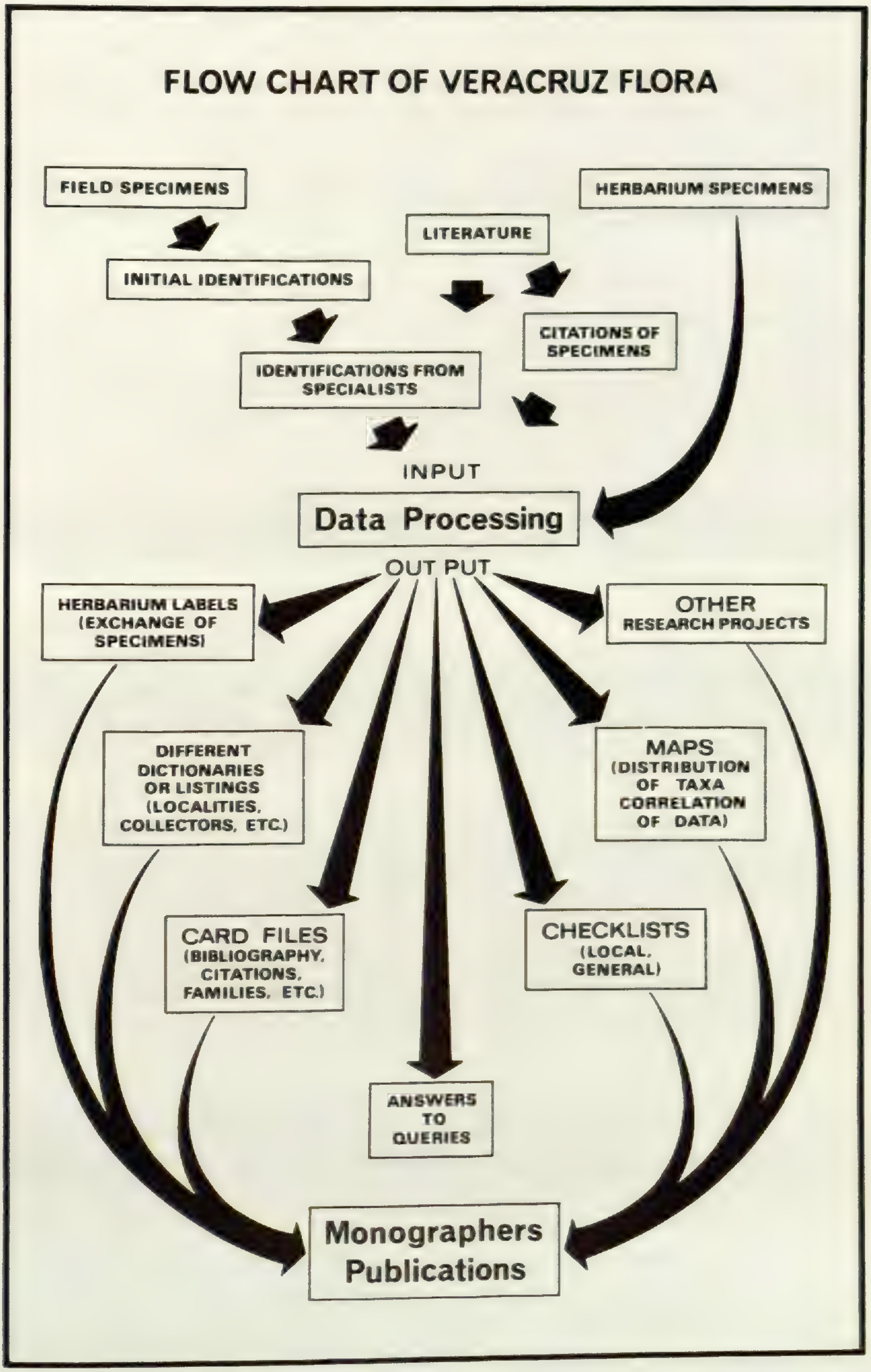

FIG. 1. Flow chart of the Flora of Veracruz.

specimen from a certain locality to the number of ovules in the ovary of a certain species collection. The main problem is to decide what is wanted and needed from the system so that it may be developed, and to concentrate on the data required. Another important aspect to be considered is the time involved in gathering the necessary data and their preparation for computer use. In our flora program, we have made the decision to use only the data for our most immediate needs; other data, for future use, has been included in free text so that they may be used if objectives change. The three main sources of data for any floristic work are: bibliographical material; field data along with specimens recently collected; and, specimens in herbaria (Fig. 1). We will describe the kinds of data we are processing and storing, how we are using them, and the techniques.[3] During the development of the computer programs we have had the generous and enthusiastic support of the personnel at the Computer Center of the UNAM, Centro de Investigación de Matemáticas Aplicadas, Sistemas y Servicios (CIMASS). We are most grateful to the Director, Dr. Renato Iturriaga, for placing facilities at our disposal.

Data from the literature. As the monumental annotated bibliography of Ida Langman (1964) for the Flora of Mexico was available, including references complete to 1950, the period for us to cover initially was self-evident; additional citations from 1950 related to the flora or those older but of great utility in the preparation of a flora. As the project includes the study of the plant resources and the environments of Veracruz, with the flora as one facet of the study, a great variety of citations are being included. The system that we are using includes the following steps:

1. Selection of the citation. Several approaches are used, including the examination of new periodicals, indices, personal card bibliographies, and retrospective examination of certain journals.

2. Selection of key words which describe the contents of a reference to be stored and by which the citation can be recalled from the computer. These include such words as: *revision, keys, illustrations, chromosomes,* etc. After the key word or words, a short free text can be added if desired; for example, *illustrations:* includes maps, photographs, and line drawings.

3. The entire citation, including journal citation presented in abbreviated form in accordance with the B-P-H system (Lawrence et al., 1968) together with its analysis and free text, is given to the bibliographer who annotates the particular family, genus, or species which is the main subject of the citation.

4. The complete citation with key words is given to a key punch operator who punches a variable set of IBM cards (Fig. 2) for each citation in a fixed format with free text. This makes it possible to include additional information for each entry and at the same time the fixed format facilitates the rapid retrieval of information.

5. The punched cards are edited and the information is transferred to

[3]Details of the format and programs are not included here.

FIG. 2. Complete set of punched cards for one bibliographic entry.

BIBLIOGRAFIA PARA LA FLORA DE VERACRUZ

TOMLINSON, P. B.1969.
ON THE MORPHOLOGY AND ANATOMY OF TURTLE GRASS,
THALASSIA TESTUDINUM (HYDROCHARITACEAE). II. ANATOMY
AND DEVELOPMENT OF THE ROOT IN RELATION TO FUNCTION.-
BULL. MAR. SCI. GULF CARIBBEAN 19:57-71.

A.L.H. HYDRC B001001
ANATOMIA ECOLOGICA
RAICES

BIBLIOTECA INST. GEOL. UNAM.

FIG. 3. Printed bibliographic card.

magnetic tapes and discs for processing. The first products the botanists see are bibliographic cards that are printed in any quantity either by the computer or by an electronic printer from the magnetic tape or from the punched cards (Fig. 3).

6. Periodically a selected bibliography for any of the key words, taxa, or any combination of them are printed as desired (Fig. 4).

7. A basic bibliographic book is printed by the computer. It consists of all the citations listed in numerical order (each citation is assigned a sequential number). This serves as a reference for queries to the computer: the answer will refer to a number in the basic book. The main reason for retrieving in this way is economic, but we are ready to develop a more sophisticated retrieval system that can be derived from files that have been constructed for this purpose.

8. Using this system we can print specialized bibliographies for our collaborators as required. Or, if we wish, we can print a cross index for the Flora of Veracruz that can be published more widely, in the same way as other abstracting publications. In our first computer generated bibliography (1971) we included more than one thousand citations. This has proven useful, not only for studies of the Veracruz flora, but for other projects as well.

There are several other possibilities in bibliographic search that we are exploring. Among these is the citation of revisions in which specimens from Veracruz and the herbaria where they may be found are cited. Because of updating possibilities in the herbarium, we included a key phrase "specimen citation" to identify these references.

Data from recent collections. We are giving emphasis to new field collections, even though many collections have been made previously in Veracruz. Unfortunately, the previous coverage is uneven as collecting was limited to a few heavily collected areas. Because of this and the need for new documentation, especially for the distribution of the taxa, a considerable number of specimens are being collected.

As most of these collections are made under our auspices, we can control the label format and data presented. A field label was designed that meets our requirements but does not place an additional burden on the collectors (Fig. 4). The field labels consist of an original and two carbons; the original is kept in a master file and one carbon copy is allotted to each of the two cooperating institutions.

The system for specimen data flow requires the following steps:

1. The collector completes the field labels for each collection number. In general, the data included are the same as those normally recorded. The only additional item necessary is to code the locality according to a grid coordinate system (Gómez-Pompa & Nevling, 1967). This particular coded entry permits the automatic printing of distribution maps.

2. The plants, with accompanying field labels, are identified.

3. The identification is recorded in the master file and the label data are prepared for card punching. This involves the assignment of a number for each collection and a numerical code for the genus and species. The genus number is derived from Dalla Torre & Harms (1900–07). If the genus is not included in that publication, a number is assigned arbitrarily, following the last generic number of the family. The species number is completely arbitrary and we keep a check list of species names with this information (Fig. 5). All important data fields must be filled, e.g., collector's name, number, and date, etc.

4. The completed label then goes to the key punch operator and the information on each label is transferred to IBM cards. Each card is numbered in sequence, and for each entry on the label there is a card (Fig. 6). All information is punched in free text within each field which makes it simple for the operator and for revision. The final item is a replication number containing the number of duplicate labels to be printed.

No. REC. INF.		FAM.
NOMBRE CIENTIFICO		
PAIS	ESTADO	MUNICIPIO
LOCALIDAD		
		MAPA
LATITUD	LONGITUD	ALTITUD
TIPO VEGETACION		PRIM. ☐ SEC. ☐
INF. AMBIENTAL		
SUELO		
ASOCIADA		
ABUNDANCIA	FORMA BIOLOGICA	TAMAÑO
AN. ☐ PERENNE ☐	OTROS DATOS	
FRUTO		FLOR
NOMBRE LOC.		FECHA COL.
USOS		DET.
COL.		No.

ORIGINAL

FIG. 4. Field label.

RANUNCULACEAE
****

ANEMONE MEXICANA HBK.	RANUN	21	1
CLEMATIS CARACASANA DC.	RANUN	22	4
CLEMATIS DIOICA L.	RANUN	22	1
CLEMATIS GROSSA BENTH.	RANUN	22	2
CLEMATIS SERICEA HBK.	RANUN	22	3
DELPHINIUM AJACIS L.	RANUN	19	1
RANUNCULUS CYMBALARIA PURSH	RANUN	26	7
RANUNCULUS DICHOTOMUS MOC. & SESSE	RANUN	26	1
RANUNCULUS GEOIDES HBK.	RANUN	26	2
RANUNCULUS HOOKERI SCHLECHT.	RANUN	26	6
RANUNCULUS MACRANTHUS SCHEELE	RANUN	26	3
RANUNCULUS PERUVIANUS PERS.	RANUN	26	8
RANUNCULUS PILOSUS HBK.	RANUN	26	4
RANUNCULUS SIBBALDIOIDES HBK.	RANUN	26	5
THALICTRUM GIBBOSUM LEC.	RANUN	28	1
THALICTRUM STRIGILLOSUM HEMSL.	RANUN	28	2

FIG. 5. Family listing from checklist prepared by computer.

5. After editing and any necessary revision of the cards, a file is generated according to a prepared program, and the labels are produced for the duplicate specimens (Fig. 7).

6. With the information stored on the files it is possible to do many things with the aid of the computer: update the checklist; construct listings of collectors, localities, collector's numbers, etc. With appropriate software, a closed information system can be prepared if needed. We intend to print a basic collection book periodically with the collection data arranged numerically with a cross index at the end for the most important items.

7. The basic collection book serves as the *base* for queries to the computer. The answer is obtained faster and more cheaply by referring to the numbers in the book. This method of information retrieval is economical: the coding is done by the computer, the search for specific information is faster, it eliminates the inclusion of information that is not reliable; *all* the information is kept for future use in case a need for it develops. More sophisticated systems can be developed from this one if desired.

8. The use of the locality files (gazetteer) permits the automatic printing of distribution maps by a plotter.

9. If the data are to be used for a specific research project, programs can be written especially for that purpose. There are numerous possible ways of presenting data in relation to specimens, such as voucher specimens for chemical, genetic, and ecological studies that are being done in the flora program or that are mentioned in the literature. Our system is open and we can add as many data cards to any collection as necessary, including bibliographic citations. Errors can be corrected in the archives at any time and will assist in keeping the data current.

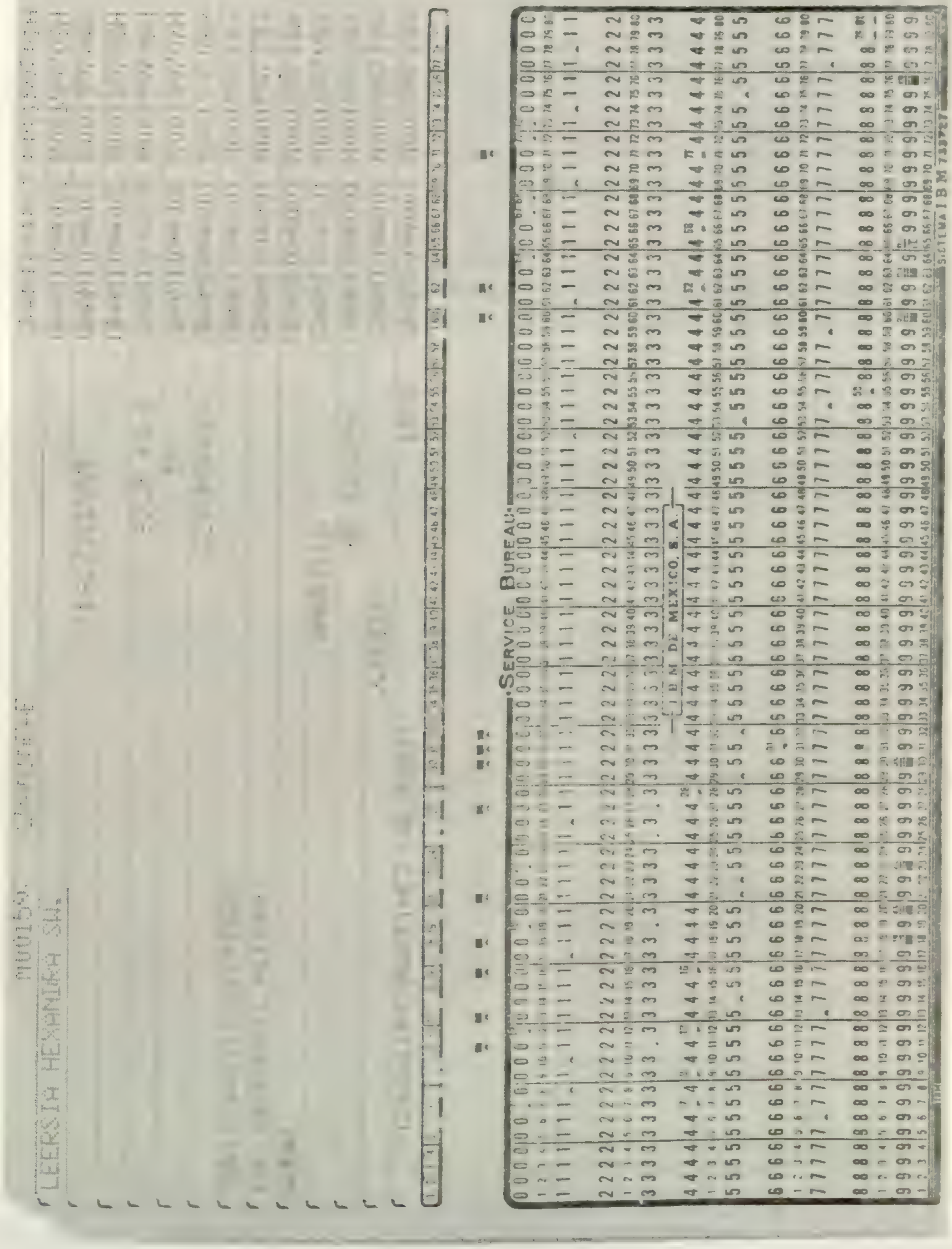

FIG. 6. Punched cards for one specimen label.

The most important source of data for any floristic project is the specimens deposited in herbaria. Representation of a particular floristic area varies from herbarium to herbarium and this poses a serious information restriction. The organization of the herbaria of the world is such that it makes it impossible to use all the information (specimens) available from an area. We have begun a retrospective search for specimen data in our respective institutions (UNAM and Harvard) and in herbaria with personnel interested in cooperating. This procedure represents a compromise but it is hoped that the coverage can be increased gradually. After a few pilot trials (Scheinvar et al., 1967; Gómez-Pompa & Olvera, 1967) we decided that the simplest procedure was to follow the same format that was developed for the field labels of current collections. As done previously, the data are presented in free text. This method overcomes the difficulties normally encountered in dealing with multiple languages.

Two main problems are posed in organizing these older materials. The first is the locality names, as some of the older specimens are attributed to place names no longer in use, or which are known under several alternate spellings. To solve this problem, we compiled a gazetteer (Gómez-Pompa & Nevling, 1970) including localities of botanical interest, coded according to our grid system (Fig. 8). The second problem is the accuracy of the identifications: at the moment we are not attempting a broad-scale revision of these. Instead, we are capturing the data on the labels, and changes in identification can be done at a later time from the archives via teletype. By using this approach, we will have a large quantity of data which will be useful in family treatments, the future Flora of Mexico, and other related research projects.

In the future, we hope to uncover and correct other data from old voucher specimens, such as misidentifications. The possibilities of using the herbarium data for different purposes have been mentioned and demonstrated in other publications (Scheinvar & Gómez-Pompa, 1969; von Reis, 1962).

A pilot project is being done at the Royal Botanic Garden, Kew, with some selected families to test the feasibility of expanding our coverage of Veracruz specimens. This test has been made possible through the generous cooperation of Ms. Laura Vit under the sympathetic and technical supervision of Dr. David Hunt.

Other Specialized Projects

Other research projects in the Flora of Veracruz series also are contributing to broaden the coverage of the data bank. One example is the study of the climatic changes in Veracruz done by Soto (1969) with the aid of the computer. All the meteorological data used for this study is in machine readable form and will be helpful in looking for correlations of plant distribution with certain climatic factors. On a broader scale it should be helpful in more precisely correlating vegetation and species with climate.

INSTITUTO DE BIOLOGIA
HERBARIO NACIONAL DE LA UNIVERSIDAD DE MEXICO (MEXU)

NO.REC.INF. D001826 COMPOSITAE

EUPATORIUM COLLINUM D.C.

CATEMACO

CARRETERA COYAME

MAPA 22.0 57.0
ALT. 300M
VEG.SECUNDARIA

ACAHUAL

SUELO ARCILLA Y GRAVA

ABUND.REGULAR HIERBA REPADORA TAM.2.50M
ANUAL LAS FLORES SON AROMATICAS

BLANCA

03/02/1969

COL.GUADALUPE MARTINEZ CALDERON NO. 1848

INSTITUTO DE BIOLOGIA
HERBARIO NACIONAL DE LA UNIVERSIDAD DE MEXICO (MEXU)

NO.REC.INF. D001880 COMPSOITAE

EUPATORIUM COLLINUM DC.

CATEMACO

CARRETERA A COYAME

MAPA 21.5 55.5
ALT. 300M
VEG.SECUNDARIA

ACAHUAL

SUELO ARCILLA Y GRAVA

ABUND.REGULAR HIERBA TREPADORA TAM.2.50M
LAS FLORES SON AROMATICAS

BLANCA

03/02/1969

COL.GUADALUPE MARTINEZ CALDERON NO. 1848

Fig. 7. Duplicate labels prepared by computer.

INSTITUTO DE BIOLOGIA
HERBARIO NACIONAL DE LA UNIVERSIDAD DE MEXICO (MEXU)

NO.REC.INF. D001826 COMPOSITAE

EUPATORIUM COLLINUM D.C.

CATEMACO

CARRETERA COYAME

MAPA 22.0 57.0
ALT. 300M
VEG.SECUNDARIA

ACAHUAL

SUELO ARCILLA Y GRAVA

ABUND.REGULAR HIERBA REPADORA TAM.2.50M
ANUAL LAS FLORES SON AROMATICAS

BLANCA

03/02/1969

COL.GUADALUPE MARTINEZ CALDERON NO. 1848

INSTITUTO DE BIOLOGIA
HERBARIO NACIONAL DE LA UNIVERSIDAD DE MEXICO (MEXU)

NO.REC.INF. D001826 COMPOSITAE

EUPATORIUM COLLINUM D.C.

CATEMACO

CARRETERA COYAME

MAPA 22.0 57.0
ALT. 300M
VEG.SECUNDARIA

ACAHUAL

SUELO ARCILLA Y GRAVA

ABUND.REGULAR HIERBA REPADORA TAM.2.50M
ANUAL LAS FLORES SON AROMATICAS

BLANCA

03/02/1969

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IDOLO	MAPA 67.0/21.0
IDOLO ISLA DEL	MAPA 66.5/20.5
IGNACIO ALTAMIRANO	MAPA 51.0/25.5
IGNACIO DEL ROSARIO	MAPA 38.0/26.5
IGNACIO DE LA LLAVE	MAPA 26.0/42.0
IGNACIO MUNOS	MAPA 52.0/25.0
IGUANARA	MAPA 14.0/65.0
INDEPENDENCIA	MAPA 46.0/27.0
INDEPENDENCIA	MAPA 44.0/25.0
INDEPENDENCIA	MAPA 39.5/24.5
INDIO	MAPA 15.0/53.0
INFIERNILLO	MAPA 32.0/40.5
INFIERNILLO	MAPA 26.0/40.5
ISLA BLANQUILLA	MAPA 33.5/41.0
ISLA DE BURROS	MAPA 71.0/18.5
ISLA DE ENMEDIO	MAPA 32.0/43.0
ISLA DE JUAN ROSAS	MAPA 50.5/23.5
ISLA DE LOS PAJAROS	MAPA 68.0/21.0
ISLA DE LOBOS	MAPA 67.5/24.0
ISLA DEL FRONTON	MAPA 72.5/17.5
ISLA DEL TORO	MAPA 69.0/19.5
ISLA FRIJOLES	MAPA 68.5/21.0
ISLA MARTINICA	MAPA 70.5/18.5
ISLA MATACABALTOS	MAPA 68.5/20.0
ISLA PAJAROS	MAPA 33.0/41.0
ISLA SACRIFICIOS	MAPA 33.0/41.0
ISLA SALMENDRA	MAPA 31.5/43.0

FIG. 8. Partial page of gazetteer with grid system coding.

Conclusion

Our experience with using electronic data processing methods for a flora project generally is very favorable. We have proof that it is very helpful and the evidence suggests that it will be even more helpful in the near future. We have been able to produce duplicate herbarium labels, bibliographic cards, bibliographic indices, checklists, maps, gazetteers, specialized data for specific research projects (Gómez-Pompa, in press) and have created a data bank that will be of great usefulness in the future. One of the things we have accomplished is to have a flexible and simple system, which is useful from the beginning. Our system is not expensive (very little computer time is required) and it will be of maximum help to the researchers of our flora who prepare family treatments. Our final objective is to write the Flora and a side product of it will be the creation of a data bank for future programs.

Machines used. During the development of our work, we have had access to a variety of machines that have been used to perform different portions of our data processing program. From the beginning we used the computers available at the UNAM computer center (CIMASS): a CDCG20 and a CDCG15 but in the last three years we have been using a Burroughs 5500 and a 6500.

For primary data input, we have used IBM 80 column punched cards. The maintenance of the files has been by means of a teletype unit. We have used an IBM 447 tabulator machine and a UNIVAC printer for inexpensive printing of certain files and for printing labels and bibliographic cards when the high speed printer of the computer was not available.

For making distribution maps, we have used a CALCOMP machine linked to an IBM computer. This machinery, as well as help and advice, was supplied by the Mexican Oil Company (PEMEX) to whom we are most grateful. The outline of our map was prepared by an OSKAR machine of the UNAM computer center.

Programming. Specific programs have been prepared for the Flora by our different programmers in the last few years. During this time we have had the advice of the staff of CIMASS who have shown a continuing interest in our project. We are indebted especially to Juan Antonio Toledo for his advice and dedication to this program. We would be very happy to give advice on this subject to any floristic project interested in our results.

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A SYSTEMATIC REVIEW OF THE SUBTRIBE MELAMPODIINAE (COMPOSITAE, HELIANTHEAE)[1]

TOD F. STUESSY[2]

In the course of recent revisionary studies on selected genera of the subtribe Melampodiinae (Stuessy 1969, 1970a, 1971a, 1972, in press), the difficulties encountered in determining generic relationships were realized to be, at least in part, symptomatic of the changing generic composition of the subtribe as well as of its morphological and chromosomal heterogeneity. As a consequence of this realization, further studies have been initiated on the generic relationships within the subtribe. In the present paper the systematics of the Melampodiinae are reviewed from three aspects: (1) a sketch of the taxonomic history of the subtribe, including changes in generic composition that have occurred since the most recent survey of Hoffmann (1890); (2) a suggestion of new changes in the generic composition of the subtribe; and (3) an indication of generic affinities within the remaining assemblage.

TAXONOMIC HISTORY

Lessing (1830) named and described the subtribe Melampodiinae (as subtribe "Melampodieae") in his report of the Compositae in the collection of Schiede and Deppe from Mexico. Due to the restricted scope of the study, the subtribe included only two genera, *Polymnia* and *Melampodium*, and it was described as follows (p. 149): "Rhachis [=receptacle] bracteolata. Antherae ecaudatae. Capitula aut dioica aut radiata, disco masculo." Two years later in the Synopsis Generum Compositarum (1832), Lessing expanded and clarified his initial description of the Melampodiinae (p. 213): "Capitula aut dioica vel subdioica aut radiata, disco masculo et radio uniseriali, foemineo. Rhachis saepissime bracteolata, aut ubi ebracteolata, ibi achaenium obcompressum et calvum. Pappus nullus aut obsoletus et bicornis." In addition, the subtribe was subdivided into four described and named units (without assigned rank) with included genera[3] as shown below (pp. 213–217):

1. Silphieae: "Achaeniis ecorticatis aut bialatis, et apice bicornibus, aut compressis et calvis; capitulis neque dioicis, neque subdioicis; rhachide bracteolata." *Hidalgoa* Llav., *Polymnia* L., *Silphium* L.

2. Millerieae: "Achaeniis ecorticatis, exalatis, calvis, lenticularibus compressis, vel pl. obcompressis, aut angulatis, sectione transversa figuram regularem sistente; capitulis neque dioicis, neque subdioicis; rhachide

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[3]In this section on taxonomic history, the genera are listed as they were originally cited by the authors. No changes have been made to more recently adopted names.

saepe ebracteolata." *Bailleria* Aubl., *Delilia* Spreng., *Milleria* L., *Oswaldia* Cass., *Pronacron* Cass., *Riencourtia* Cass., *Trigonospermum* Less.

3. Euxenieae: "Achaeniis ecorticatis; capitulis homogamis, dioicis; rhachide bracteolata." *Astemma* Less., *Euxenia* Cham., *Phaethusa* Gaertn.

4. Melampodieae: "Achaeniis calvis, corticatis; capitulis radiatis, radio uniseriali, foemineo, disco masculo; rhachide bracteolata." *Centrospermum* Kunth, *Melampodium* L.

Several years before Lessing published his scheme of classification for the Compositae, H. Cassini published his own reorganization of the family in the many volumes of the Dictionnaire des Sciences Naturelles edited by Cuvier (1816–1830). These numerous and detailed observations were then summarized in volume three of his Opuscules Phytologiques (1834). Although in this latter work Cassini did not recognize a subtribe Melampodiinae by name, in his tribe Hélianthées, Section Millériés, his unranked "Millériées vraies" characterized by "Disque masculiflore" corresponded in large measure to the subtribe Melampodieae of Lessing (excluding the dioecious Euxenieae). Within the Millériées vraies were contained two units. The first, "Millériées vraies, régulières," with the genera *Alcina* Cav., *Centrospermum* Kunth, *Melampodium* L., *Polymnia* L., *Polymniastrum* Lam., and *Zarabellia* Cass., corresponded roughly to the subdivisions Silphieae and Melampodieae of Lessing. The second unit, "Millériées vraies, irrégulières," containing the genera *Elvira* Cass., *Meratia* Cass., *Milleria* L., *Pronacron* Cass., *Riencourtia* Cass., and *Unxia* L.f., was approximately equivalent with the Millerieae of Lessing (Table 1).

Candolle in the Prodromus (1836) modified the circumscription of the subtribe Melampodiinae established by Lessing by broadening the limits to include the genus *Ambrosia* L. and its relatives. Seven "Divisions" of the "Melampodineae" were recognized. The first four corresponded reasonably well to those subdivisions of Lessing; the last three were new additions to the subtribe (Table 1). Candolle's classification with included genera is as follows:

1. Euxenieae: *Astemma* Less., *Euxenia* Cham., *Petrobium* R. Br.

2. Millerieae: *Aiolotheca* DC., *Apalus* DC., *Chrysogonum* L., *Clibadium* L., *Elvira* Cass., *Fougerouxia* Cass., *Ichthyothere* Mart. in Buchn., *Latreillea* DC., *Milleria* L., *Pronacron* Cass., *Riencourtia* Cass., *Scolospermum* Less., *Trigonospermum* Less., *Unxia* L.f., *Xenismia* DC.

3. Silphieae: *Berlandiera* DC., *Espeletia* Mutis ex H. & B., *Guardiola* Cerv. ex H. & B., *Hidalgoa* Llav., *Polymnia* L., *Silphium* L.

4. Melampodieae: *Acanthospermum* Schrank, *Melampodium* L.

5. Ambrosieae: *Ambrosia* L., *Franseria* Cav., *Xanthium* L.

6. Iveae: *Euphrosyne* DC., *Iva* L., *Pinillosia* Ossa in DC., *Tetranthus* Sw.

7. Parthenieae: *Coniothele* DC., *Leptosyne* DC., *Mendezia* DC., *Parthenium* L., *Tragoceras* H.B.K.

TABLE 1. HISTORY OF CLASSIFICATION OF THE SUBTRIBE MELAMPODIINAE

Lessing (1832)	Cassini (1834)	Candolle (1836)	Bentham and Hooker (1873)	Hoffmann (1890)
Tribe Asteroideae	Tribe Hélianthées	Tribe Senecionideae	Tribe Heliantheae	Tribe Heliantheae
Subtribe Melampodieae	Section Milléréées	Subtribe Melampodineae		
Melampodieae →		Division* Melampodieae		
	Milléréées vraies. régulières →			
Silphieae →		Division Silphieae		
	Milléréées vraies, irrégulières →			
Millerieae →		Division Millerieae →	Subtribe Millerieae →	Subtribe Millerinae
Euxenieae →		Division Euxenieae →	Subtribe Petrobieae →	Subtribe Petrobinae
		Division Parthenieae →	(To various subtribes; *Parthenium* to Melampodieae)	
		Division Ambrosieae	Subtribe Ambrosieae →	Subtribe Ambrosinae
		Division Iveae		

*Arrows indicate continuity of concepts of subdivisions from one author to another.

Bentham and Hooker in the Genera Plantarum (1873) established the generic composition of the subtribe Melampodiinae (as well as that of the entire family) that is still in use today with but minor variations. Their subtribe "Melampodieae" was basically the Silphieae and Melampodieae of Lessing and of Candolle, and the Millériées vraies, régulières of Cassini with several other genera added. The included genera are as follows: *Acanthospermum* Schrank, *Aiolotheca* DC., *Baltimora* L., *Berlandiera* DC., *Chrysogonum* L., *Dicranocarpus* A. Gray, *Engelmannia* T. & G., *Espeletia* Mutis ex H. & B., *Guardiola* Cerv. ex H. & B., *Ichthyothere* Mart. in Buchn., *Lecocarpus* Dcne., *Lindheimera* A. Gray & Engelm., *Melampodium* L., *Parthenice* A. Gray, *Parthenium* L., *Philoglossa* DC., *Polymnia* L., *Schizoptera* Turcz., *Silphium* L., *Trigonospermum* Less. This revised group of genera was characterized by heads with sterile disc florets, large numbers of florets per head, and paleaceous receptacles. As for the other Divisions of Candolle's Melampodineae, the Millerieae and Euxenieae were made separate subtribes as the Millerieae and Petrobieae respectively, and the Ambrosieae and Iveae for the most part become the subtribe Ambrosieae (Table 1).

Hoffmann (1890) followed the classification of the Compositae of Bentham and Hooker almost exactly. The subtribe Melampodiinae was characterized as before with two additional new genera: *Dugesia* A. Gray, and *Moonia* Arn.

Since Hoffmann (1890) and Dalla Torre and Harms (1907) listed 22 genera, several generic shifts have been suggested within the Melampodiinae by various authors. Small and Carter (1913) revived the genus *Polymniastrum* Lam. as a close relative of *Polymnia*. Blake (1917a) switched *Clibadium* to the Melampodiinae from its previous inclusion in the subtribe Milleriinae. Several years later Blake (1923) added a new genus, *Rensonia,* followed by Humbert's addition of *Tisserantia* (1927), Mackenzie's addition of *Smallanthus* (in Small, 1933), and Sherff's addition of *Oparanthus* (1937), which brought the total number of genera to 28. Cronquist (1955) cancelled Humbert's addition by indicating that *Tisserantia* should be included within *Sphaeranthus* L. of the tribe Inuleae. Based on morphological and detailed anatomical data, Carlquist (1957) transferred *Oparanthus* from the Melampodiinae to the subtribe Petrobiinae. Blake (in Sandwith, 1956) indicated that *Philoglossa* probably should be moved to the subtribe Liabinae of the Senecioneae. Still later, *Polymniastrum* and *Smallanthus* were resubmerged into *Polymnia* by Wells (1965). Rzedowski (1968) reported that *Aiolotheca* DC. was congeneric with the earlier described *Zaluzania* Pers. in the Helianthinae (=Verbesininae; Solbrig, 1963), and recently *Unxia* L.f. was resurrected from out of *Melampodium* (Stuessy, 1969). Presently, then, there are 23 genera in the Melampodiinae, and these are listed in Table 2 with available studies that are at least partially comprehensive.

SUGGESTED NEW CHANGES IN GENERIC COMPOSITION

The most recent criteria of Bentham and Hooker (1873) and Hoffmann (1890) for delimiting the subtribe Melampodiinae emphasize the characters of many and sterile disc florets and a paleaceous receptacle. These features contrast with those of the neighboring and similar subtribe, the Milleriinae, which also has sterile but fewer disc florets and naked receptacles. Based on an understanding of the variation in these features that is known to occur in the Compositae (Bentham, 1873; Shull, 1902; Nakano, 1910; Small, 1919; Gleason, 1919), the reliance on these few characters alone for subtribal differentiation might be viewed with suspicion. In particular, grouping genera by the sterility of the disc florets might seem artificial, because it is likely that such a feature has evolved independently in at least several instances in the Compositae as evidenced by its occurrence in several different tribes of the family (Bentham, 1873). It is interesting to note that Linnaeus in his sexual system of classification (1735) recognized in the "Class Syngenesia" an "Order Polygamia Necessaria" that was characterized by fertile female ray florets and hermaphroditic sterile disc florets. This same grouping used by Linnaeus in the Species Plantarum (1753) contained 13 genera including *Chrysogonum*, *Melampodium*, *Polymnia*, and *Silphium*, now of the Melampodiinae.

The artificiality of the Melampodiinae, however, has not gone unnoticed, and several workers already have commented on its heterogeneous nature

TABLE 2. LIST OF REVISIONARY STUDIES OF GENERA CURRENTLY INCLUDED IN THE SUBTRIBE MELAMPODIINAE

Genus	Revisionary Studies
Acanthospermum Schrank	Blake (1921); Stuessy (1970a)
Baltimora L.	Stuessy (in press)
Berlandiera DC.	Turner and Johnston (1956); Pinkava (1967)
Chrysogonum L.	
Clibadium L.	Schulz (1912); Blake (1917a)
Dicranocarpus A. Gray	
Dugesia A. Gray	
Engelmannia T. & G.	Turner and Johnston (1956)
Espeletia Mutis ex H. & B.	Standley (1915); Smith and Koch (1935); Cuatrecasas (1949, 1954)
Guardiola Cerv. ex H. & B.	Robinson (1899)
Ichthyothere Mart. in Buchn.	
Lecocarpus Dcne.	Cronquist (1971); Eliasson (1971)
Lindheimera A. Gray & Engelm.	Turner and Johnston (1956)
Melampodium L.	Robinson (1901); Stuessy (1972)
Moonia Arn.	
Parthenice A. Gray	
Parthenium L.	Rollins (1950); Mears (1970)
Polymnia L.	Wells (1965)
Rensonia S. F. Blake	Blake (1923)
Schizoptera Turcz.	Blake (1916, 1917b)
Silphium L.	Perry (1937); Fisher (1959, 1966); Settle and Fisher (1970); Sweeney (1970)
Trigonospermum Less.	McVaugh and Laskowski (1972)
Unxia L.f.	Stuessy (1969, 1971a)

(Gray, 1855; Turner and Johnston, 1956; Turner and King, 1962; Skvarla and Turner, 1966). Despite these comments, little has been done to modify the composition of the subtribe in order to increase its homogeneity. One difficulty encountered is the necessity of having a familiarity not only with genera of the Melampodiinae, but also with those in the other subtribes of the Heliantheae. Although a survey of all genera of the tribe is beyond the scope of the present study (such a survey currently is in progress; Stuessy, in prep.), the affinities of several of the genera of the Melampodiinae to those of other more clearly defined subtribes have become apparent. In particular, *Dicranocarpus*, *Guardiola*, and *Moonia* appear to belong more properly in the subtribe Coreopsidinae, and *Parthenice* and *Parthenium* seem placed better within the subtribe Ambrosiinae.

Of all the subtribes of the Heliantheae, the Coreopsidinae as recognized by Hoffmann (1890) is one of the most cohesive. Although some genera probably are misplaced (e.g., *Calyptocarpus* Less., *Synedrella* Gaertn.), the majority of the approximately 18 genera share the following characteristics: brown-orange longitudinal traces in the phyllaries and corollas and often also in the stamens and styles of disc and ray florets;[4] scarious-margined phyllaries; deeply divided or dissected leaves; pappus of two long awns (absent in *Dahlia* Cav. and *Hidalgoa* Llav.); and chromosome numbers on an apparent base of x=12 (*Dahlia* and *Hidalgoa* are based on x=16) (Solbrig, Kyhos, Powell, and Raven, 1972).

Dicranocarpus with one species and *Guardiola* with about ten species are very similar to each other and also distinct within the Melampodiinae in possessing narrowly campanulate involucres. Both these genera have all the features of the Coreopsidinae mentioned above (except *Guardiola* is without a pappus and has only dentate leaves) including compatible chromosome numbers; *Dicranocarpus* has been counted as n=10 (Turner and Johnston, 1961), and *Guardiola* is known with n=12 (Solbrig et al., 1972). Even A. Gray, in describing *Dicranocarpus* as new (1855), pointed out the relationship to *Heterosperma* Cav. of the Coreopsidinae. The former genus, in fact, is so similar to *Wootonia* Greene of the same subtribe (earlier mentioned by Turner and King, 1962), that any serious study of either genus should include examination of the other taxon as a possible congener.

Moonia is a small, apparently monotypic, genus from India and Ceylon. Bentham and Hooker (1873) treated *Moonia* as a synonym of *Chrysogonum*, but Hoffmann (1890) reinstated it as a distinct genus. The similarity of *Moonia* to *Chrysogonum* or any other genus of the Melampodiinae is not obvious, and in fact, among the genera of the Heliantheae, it is most similar to *Dahlia* and *Hidalgoa* of the Coreopsidinae. The details of this

[4]These traces probably represent concentrations of anthochlor pigments (=chalcones and aurones) which in the Compositae are known to be distributed mainly in the Coreopsidinae (Gertz, 1938; Cronquist, 1955; Shimokoriyama, 1962).

affinity will be reported elsewhere (Stuessy, in prep.). It is sufficient to note here that *Moonia* possesses all of the characters of the Coreopsidinae mentioned above with the exception that chromosome numbers for the genus are not yet known, and no pappus is present (a feature also shared by *Dahlia* and *Hidalgoa*).

The Ambrosiinae as traditionally recognized (Hoffmann, 1890) is probably the most distinct and unified subtribe of the Heliantheae. This unity is so striking that several workers have preferred to recognize the group as a distinct tribe (Payne, 1964; Payne, Raven, and Kyhos, 1964; Skvarla and Turner, 1966). Several unique features are shared by all genera of the Ambrosiinae (in part from Payne, Raven, and Kyhos, 1964): alternate leaves; nodding flowering heads; sterile hermaphroditic florets with rudimentary, unbranched styles; anemophilous mode of pollination; free, short and translucent anthers with hooked appendages; bladder-like air chambers of the pollen walls; and chromosome numbers on a base of x=18.

Parthenium with 13 species (Rollins, 1950) and the monotypic *Parthenice* have been recognized by many workers as having affinities with the Ambrosiinae. *Parthenice*, in fact, was placed by A. Gray at the time of original description (1853) between *Parthenium* and *Euphrosyne* (of the Ambrosiinae) with the comment (p. 85) that *Parthenice mollis* has ". . . much the aspect of *Euphrosyne xanthifolia*. . . ." Even Bentham in the discussion of his new classification of the Compositae (1873; p. 435) wrote that the Ambrosiinae ". . . are, without a doubt, connected with *Artemisia* as well as with Melampodineae, having much of the habit of the former and passing into the latter through *Parthenice;* but geographically, as well as structurally, the relationship to Melampodineae appears to me to be the closest." Since that time, several workers have continued the commentary on the relationships of *Parthenium* and *Parthenice* with the Ambrosiinae (e.g., Rollins, 1950; Alston and Turner, 1963; Skvarla and Larson, 1965; Skvarla and Turner, 1966), but no one has suggested yet that both genera should be moved from their present position in the Melampodiinae. In my opinion, little question exists that *Parthenium* embraces *Parthenice* as its closest relative. Both genera have little in common with other genera of the Melampodiinae, and both possess characteristics of the Ambrosiinae particularly in features of the leaves, anthers, and styles. In addition, the chromosome numbers of *Parthenium* (*Parthenice* has not yet been counted) coincide with those of genera in the Ambrosiinae. Three of the four sections of *Parthenium* are known chromosomally to have base numbers of x=18 [section *Argyrochaeta* (Cav.) DC. seems based on x=17][5] (Rollins, 1950; Mears, 1970), and therefore the base number for the whole genus seems likely to be x=18. Recent anatomical studies of seedling anatomy (Anderson, 1970, pers.

[5]Three of the five species in this section have been counted chromosomally, and two of them, *P. confertum* A. Gray and *P. hysterophorus* L., are clearly based on x=17 (n=36 and 34, and n=17 respectively). *P. bipinnatifidum* (Ortega) Rollins, however, has been reported from five populations as n=12 (Rollins, 1950).

comm.) also support the relationship of *Parthenium* to the Ambrosiinae. Of the 13 genera[6] of the subtribe Melampodiinae that have been sampled, *Parthenium* is the only genus that has two traces associated with the midveins of the cotyledons—the same situation found in *Xanthium* L. of the Ambrosiinae. Electron microscopic studies of pollen grains also reveal the similarity of large cavea and internal foramina in the ektexine of *Parthenium* and genera of the Ambrosiinae (Skvarla and Larson, 1965; Payne and Skvarla, 1970), but *Parthenice* in palynological features is somewhat different from both these taxa. Recent chemical studies, although of a limited nature, also help substantiate the relationship of *Parthenium* to the Ambrosiinae. The sesquiterpenoid compound hymenin, previously known only from *Hymenoclea* T. & G. in the Ambrosiinae, now has been discovered in *Parthenium* (Rodriguez, Yoshioka, and Mabry, 1971). In addition, three other sesquiterpenoids (ambrosin, coronopilin, and parthenin) have been found in *Parthenium* as well as in genera of the Ambrosiinae (Mitchell and Dupuis, 1971): *Ambrosia* (all three compounds); *Hymenoclea* (ambrosin); and *Iva* (coronopilin and parthenin).

The most conflicting datum in moving *Parthenium* and *Parthenice* to the Ambrosiinae is the presence of an "achene-complex" (Rollins, 1950) in both genera as well as in the melampodioid genera, *Berlandiera, Chrysogonum, Engelmannia,* and *Lindheimera.* This unusual morphological feature of the capitulum is a basally fused complex of one phyllary, one fertile female ray floret, two sterile hermaphrodite disc florets, and two to four receptacular paleae.[7] Such a structure is indeed unusual enough to suggest strongly that *Parthenium* and *Parthenice* must be related in some way to these other genera of the Melampodiinae, especially because *Parthenium* does show some overall morphological resemblance to *Engelmannia.*

Because of the relationship of *Parthenium* and *Parthenice* to both the Melampodiinae and Ambrosiinae, and because of the morphologically specialized and polyploid condition of the latter subtribe, one might speculate that the Ambrosiinae *s. str.* was derived from a *Parthenium*-like ancestor which in turn came from an *Engelmannia*-like progenitor (Fig. 1). The ancestor of the entire generic assemblage may have been based on $x=9$, with one main line then leading directly to *Engelmannia,* another line leading by aneuploid reduction ($x=8$) to other genera of the Melampodiinae, and a polyploid third line ($x=18$) to the Ambrosiinae *(s. l.).* These hypothetical relationships are compatible with the morphological and cytological data obtained by Payne, Raven, and Kyhos (1964) and with the ultrastructural features of pollen grains reported by Skvarla and Larson (1965).

[6] *Acanthospermum, Baltimora, Berlandiera, Chrysogonum, Clibadium, Engelmannia, Espeletia, Guardiola, Lindheimera, Melampodium, Parthenium, Polymnia,* and *Silphium.*

[7] In the achene-complex of *Parthenice* the outer phyllaries are closely associated but not fused basally with the ray achenes.

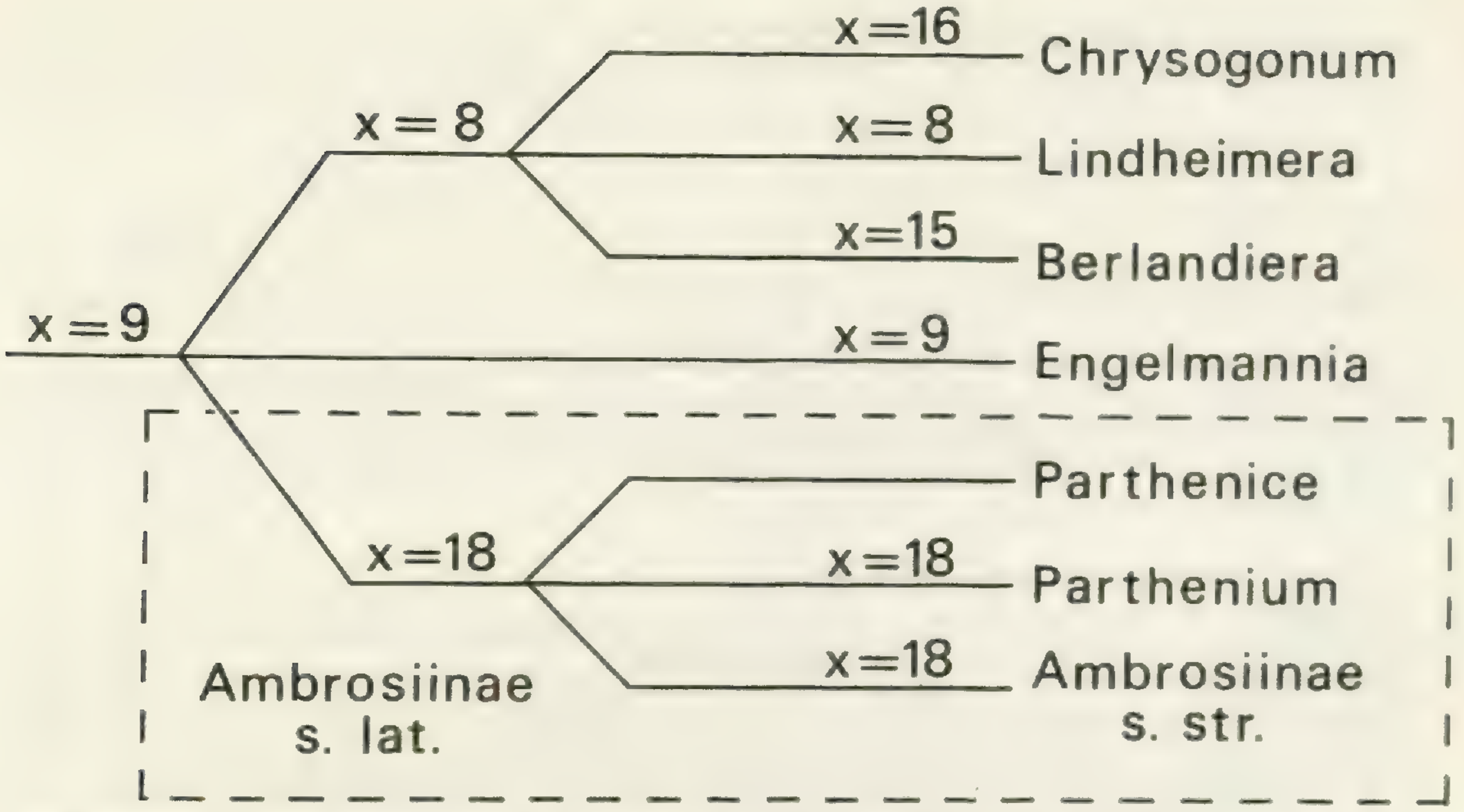

FIG. 1. Hypothetical evolutionary relationships among *Chrysogonum*, *Lindheimera*, *Berlandiera*, and *Engelmannia* of the Melampodiinae, and *Parthenice*, *Parthenium*, and the Ambrosiinae *s. str.*

The clarification of the evolutionary affinities of these taxa, although providing a better understanding of the biological relationships, poses a problem in classification. One might believe that because the entire generic complex shown in Fig. 1 is monophyletic, it should be treated as a separate subtribe of the Heliantheae. However, this alternative seems undesirable because the genera of the Ambrosiinae *s. str.* have many distinct features that are not found in the other four genera of the Melampodiinae. To leave the situation unchanged also seems unsatisfactory in view of the very strong similarity of *Parthenium* and *Parthenice* to the Ambrosiinae. In my opinion, the best alternative is to move *Parthenium* and *Parthenice* into the Ambrosiinae *s. l.*[8] The remaining genera seem best left for the present as a natural group of the Melampodiinae that may or may not have close relatives in other subtribes. If with further investigations no additional relatives are discovered, then the recognition of these genera as a small subtribe of the Heliantheae may be in order. Obviously, the solution to this problem must await the completion of studies on the subtribal limits of the entire tribe (Stuessy, in prep.).

GENERIC AFFINITIES

The removal of *Dicranocarpus*, *Guardiola*, *Moonia*, *Parthenice*, and *Parthenium* from the Melampodiinae still leaves a very heterogeneous assemblage of 18 genera. The diversity of morphological and chromosomal features that exist among these taxa is so great that it emphasizes again the

[8]Although it is not intended here to evaluate in detail the desirability of tribal status for the Ambrosiinae (either as *s. str.* or *s. l.*), the evolutionary relationships of the Ambrosiinae to *Engelmannia*, etc., suggest that such a disposition is unwarranted (for agreement see Bentham, 1873; Small, 1919; Cronquist, 1955).

TABLE 3. CHROMOSOME NUMBERS OF GROUPS OF GENERA OF THE SUBTRIBE MELAMPODIINAE

Group	Genus	Known chromosome numbers (n)	Probable base number (x) of genus	Probable base number (x) of generic group
1	Clibadium L.	16, 24	8	8
	Ichthyothere Mart. in Buchn.	ca. 33	32	
2	Espeletia Mutis ex H. & B.	19	19	16
	Polymnia L.	15, 16, 17, ca. 20, 29, 30, 33±1	15, 16	
	Unxia L.f.	16	16	
3	Baltimora L.	15	15	15
	Trigonospermum Less.	15	15	
4	Acanthospermum Schrank	10,11	11	10, 11
	Lecocarpus Dcne.	11	11	
	Melampodium L.	9, 10, 11, 12, 18, 20, 23, 25±1, 27, 30, 33	10	
5	Dugesia A. Gray	18	18	7, 8, 9
	Rensonia S. F. Blake	–	–	
	Schizoptera Turcz.	–	–	
	Silphium L.	7, 8	7	
6	Berlandiera DC.	15	15	9
	Chrysogonum L.	16	16	
	Engelmannia T. & G.	9	9	
	Lindheimera A. Gray & Engelm.	8	8	

polyphyletic nature of the group and the necessity of looking to other subtribes for suitable generic relatives. In view of the limited scope of the present study, the best solution that can be offered at this time is simply to point out groupings of what appear to be closely related genera within the subtribe. These units eventually may prove to have strong affinities with generic clusters in other subtribes. Six such informal groups have been recognized here in the Melampodiinae and these are shown together with available chromosomal data in Table 3. The chromosome numbers

have been obtained from the following indexes and references: Darlington and Wylie (1955); Cave (1958–65); Ornduff (1967–69); Coleman (1968, 1970); Fedorov (1969); Powell and King (1969); Powell and Cuatrecasas (1970); Moore (1970–71); Stuessy (1970b, 1971b); Solbrig et al. (1972).

The two genera of group one, *Clibadium and Ichthyothere*, are closely related South American taxa that have very short, tubular ray corollas, and small, narrow anthers, uniform in color with acute appendages. As Blake emphasized earlier (1917a, p. 2), the two genera are so similar that ". . . it seems beyond dispute that *Clibadium* should be removed from the *Millerinae* and referred to the *Melampodinae* next to *Ichthyothere*, ..." Although chromosome numbers for both genera are available only from several out of a large number of species (ca. 30), the counts at hand of n=16, 24, and ca. 33 suggest a common base of x=8.[9] Because only one species of *Ichthyothere* has been counted, it is impossible to know whether x=32 is the base for the genus (as suggested in Table 3) or, if upon accumulation of additional reports, x=16 or x=8 might prove to be basic. As for close generic relatives outside the Melampodiinae, *Desmanthodium* Benth. of the Milleriinae seems very similar, but affinities of these three genera with other taxa are uncertain. Chromosome counts for *Desmanthodium* have not yet been obtained.

Group two includes three genera of close affinity: *Espeletia*, *Polymnia*, and *Unxia*. *Espeletia* is a common member of the Andes of Colombia and Venezuela, *Unxia* is restricted to the northern portion of South America, and *Polymnia* ranges from South America to the eastern United States. All three genera have black, glabrous to subglabrous, subglobose fruits with no pappus. In addition, the ray achenes are partially enclosed by (but not fused with) the inner row of phyllaries. *Unxia* for many years was considered a synonym of *Melampodium* (Bentham and Hooker, 1873; Hoffmann, 1890), but recently the former genus has been reestablished as a close relative of *Polymnia* (Stuessy, 1969). The available chromosome numbers for these genera point clearly to a base of x=16 for both *Unxia* and *Polymnia*. The n=19 counts obtained from about 30 species of *Espeletia* (Powell and King, 1969; Powell and Cuatrecasas, 1970) may have originated by aneuploid gain from an x=16 base for the entire complex of three genera. Many additional counts obviously are needed, especially because *Espeletia* is a large genus with perhaps as many as 74 species (Cuatrecasas, 1954).

The two genera of group three, *Baltimora* and *Trigonospermum*, seem

[9]Coleman (1968) was the first to suggest this base number for the genus founded mainly on his new count of n=24. The camera lucida drawing of the meiotic configuration of the species counted, *C. armanii* Sch. Bip., shows 16 large and eight very small chromosomes, which gives strong support to the x=8 hypothesis. The eight chromosomes are so small, however, that Coleman mentions (p. 232) the ". . . possibility that the 8 smaller chromosomes are B chromosomes. . . ." If these chromosomes do indeed prove to be supernumeraries, which are often variable in number within a taxon, then this reported count would be less substantial support for an x=8 base.

to be closely related in their annual habit, triquetrous fruits, and chromosome numbers of n=15 (Stuessy, in press). However, *Baltimora* also shows some relationship to *Wedelia* Jacq. of the Helianthinae (=Verbesininae), and *Trigonospermum* is similar to *Sigesbeckia* L. of the same subtribe (corroborated by McVaugh and Laskowski, 1972). It would not be surprising, therefore, that after a more careful appraisal of generic relationships in the entire tribe, these two genera justifiably might be separated.

Group four includes three genera that have inner involucral bracts each enclosing and fused with individual ray achenes. *Melampodium* is the largest (37 species currently recognized; Stuessy, 1972), most morphologically diverse of the generic trio, and with a distribution centering in Mexico and Central America. *Acanthospermum* contains six species (Stuessy, 1970a) and ranges mainly throughout Latin America with scattered introductions to parts of the Old World (Blake, 1921). *Lecocarpus* is the smallest and most restricted genus of the group with three species that are endemic to the Galápagos Islands (Cronquist, 1971; Eliasson, 1971). Chromosomal data supplement the morphological unity of these genera. *Acanthospermum* and *Lecocarpus* are clearly on a base of x=11, but *Melampodium*, for reasons explained elsewhere (Stuessy, 1971b), seems more likely to be based on x=10. The ancestral base for the entire complex, therefore, could have been either x=10 or x=11, although the former number has been suggested previously (Stuessy, 1971b). The relationship of these taxa to other genera of the Heliantheae is obscure at present. Other taxa such as *Rumfordia* L., *Sigesbeckia*, and genera of the subtribe Madiinae also have phyllaries enclosing (but not fused with) ray florets. Whether these similarities reflect parallelisms or homologies remains to be determined, but because of the otherwise divergent morphologies of these taxa, it seems likely that the former condition has prevailed.

The genera of group five, *Dugesia, Rensonia, Schizoptera*, and *Silphium*, form an interesting but probably heterogeneous group of taxa that have dorsally flattened and laterally winged achenes. Within the Melampodiinae these genera do comprise a comfortable morphological unit, but upon examining genera in other subtribes such as the Helianthinae (=Verbesininae), the very close relationship of some of these taxa makes the cohesiveness of group five less striking. For example, the monotypic *Rensonia* is very similar to *Wedelia*. This similarity is particularly interesting because one species of the latter genus, *W. parviceps* S. F. Blake, has sterile disc florets and is found in the same geographic region (i.e., Central America) as *Rensonia salvadorica* S. F. Blake. As a result of a lack of clear understanding of these relationships at this time, the proposed base numbers for the group (x=7, 8, or 9) should be viewed with considerable scepticism.

Berlandiera, Chrysogonum, Engelmannia and *Lindheimera* comprise generic group number six. All four genera are distributed mainly in the

southern United States and adjacent Mexico,[10] and all have conspicuous, elliptic ligules, dissected or at least lobed leaves, and "achene-complexes" (=a basally fused ray achene, inner phyllary, and 2–4 paleae with included sterile disc florets). Based on this latter feature, *Parthenium* and *Parthenice* might be included here, but for reasons explained earlier in this paper, these genera seem best placed in the Ambrosiinae. The chromosome numbers for all four genera of this group are diverse with n=8, 9, 15, and 16. A base of x=9 is suggested for the entire generic complex with *Engelmannia* (n=9) retaining the ancestral number (Fig. 1). The other three genera are believed to have evolved from an aneuploid base of x=8. *Lindheimera* may have developed without change in chromosome number from the immediate ancestor, but *Chrysogonum* seems an obvious polyploid with n=16 and *Berlandiera* seems interpreted best as an aneuploid at the tetraploid level with n=15.

Conclusion

The observations presented here reveal again that the subtribe Melampodiinae is morphologically heterogeneous and clearly polyphyletic (already mentioned by several writers, e.g., Gray, 1855 ["an incongruous group," p. 321]; Turner and Johnston, 1956; Turner and King, 1962; Skvarla and Turner, 1966). The characters of large numbers of disc florets and the presence of disc paleae have been emphasized to the exclusion of many other features. Even though most of the genera of the Melampodiinae are now reasonably well known, the needed critical realignment of the taxa cannot be accomplished without first obtaining a better understanding of the limits and affinities of genera in the other subtribes, particularly in the Helianthinae (=Verbesininae). This latter assemblage of 58 genera (as recognized by Hoffmann, 1890) is very much in need of treatment. The subtribe Milleriinae also needs to be understood better from a generic standpoint (Stuessy, 1971a), for taxa such as *Desmanthodium* show obvious affinities with *Clibadium* and *Ichthyothere* in the Melampodiinae.

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[10]Several species of *Chrysogonum* have been described from Madagascar and others from Ceylon and Australia. The proper disposition of these taxa is not clear, but they seem only distantly related to the type species, *Chrysogonum virginianum* L. of the southeastern United States.

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A REVISION OF THE FERN GENUS NEPHELEA

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The genus *Nephelea* comprises a major evolutionary group of tropical American tree ferns. Because it was only recently recognized as a taxon, *Nephelea* lacks the long and often complex taxonomic history associated with many fern genera. It was described for the first time by Tryon (1970) as a result of a complete and long-overdue generic revision of the Cyatheaceae in which eight genera, representing natural evolutionary lines, were recognized. These eight genera are *Metaxya* and *Lophosoria* with trichomes but without scales on the stem and petioles, and *Sphaeropteris, Alsophila, Nephelea, Trichipteris, Cyathea,* and *Cnemidaria* with scales and with or without trichomes on the stem and petioles. Usually the large bulk of the squamate members of the Cyatheaceae had previously been treated in the three classical and unnatural genera, *Cyathea, Hemitelia,* and *Alsophila,* based solely on characters of the indusium. Recognizing the unnaturalness of these classical genera, Copeland (1947) proposed a nearly inclusive genus *Cyathea* (ca. 800 species) and four minor genera (*Trichopteris, Cnemidaria, Gymnosphaera,* and *Schizocaena*–totaling about 50–60 species). These were purportedly natural lines based largely on stem development, degree of leaf dissection, color of axes, articulation of pinnae, venation, and presence or absence of an indusium. Holttum (1963) circumscribed the Cyatheaceae in an inclusive sense with a more rigorously defined genus *Cyathea.* He recognized *Cnemidaria* as the only other genus among the squamate genera of the Cyatheaceae. Before the recognition of *Nephelea* as a natural alliance of generic rank, most of its species had been described in the genus *Cyathea,* two had been placed in *Hemitelia,* six erroneously in *Alsophila,* and one in the non-squamate genus *Lophosoria.*

The name of the genus is derived from the greek *νεφέλη* (nephéle) in reference to the usual cloud forest habitat of its species. Species occur in the Greater and Lesser Antilles and from Mexico to Argentina and eastward in South America to Venezuela and French Guiana in the north and to Paraguay and Brazil in the south (Map 1). *Nephelea* exhibits a broad altitudinal distribution from sea level *(N. cuspidata)* to 2800 m. *(N. erinacea* var. *purpurascens).*

GENERIC AFFINITIES

A key to the genera of the Cyatheaceae has been provided by Tyron (1970, pp. 14–16). This key and its accompanying discussion should be consulted for general generic determinations and for a thorough treatment of the generic characters employed. For use in identification and as an orientation to *Nephelea* itself, a synoptical arrangement of the key is

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given below together with reference to illustrations that emphasize certain points.

A. Stem and petioles with trichomes, scales absent ..... *Lophosoria, Metaxya.*
A. Stem and petioles with scales, trichomes present or absent on the petioles ..... B.
B. Petiole scales structurally conform, the cells of the body similar in orientation, shape, and (usually) in size and color (Figs. 1, 2) ..... *Sphaeropteris.*
B. Petiole scales structurally marginate, with a narrow to broad margin of cells different in orientation, size, and (usually) in shape and color from those of the central portion (Figs. 3, 4) ..... C.
C. Petiole scales (or some of them) with a dark (very rarely lighter colored) apical seta, similar setae sometimes also borne on the body of the scale or on its edge (Figs. 66, 79) ..... D.
D. Petiole lacking spines, smooth to tuberculate, or with corticinate spines (Fig. 5), unexpanded croziers lacking spines; scales of the petiole (especially on the abaxial side) more or less appressed, attached at a thickened base or usually at one point of a pseudopeltate or peltate base ..... *Alsophila.*
D. Petiole with squaminate spines, many large, black, mostly obturbinate with a slender apex (Figs. 6, 16, 17), small spines bear differentiated margins like the scales (Figs. 7–9), the unexpanded croziers with well developed squaminate spines (Figs. 6, 16, 17), many of them caducous ..... *Nephelea.*
C. Petiole scales lacking apical setae, the apex rounded to filamentous (Figs. 10, 11) ..... *Trichipteris, Cyathea, Cnemidaria.*

Evidence that *Nephelea* is most closely related to *Alsophila* is found not only in the unique common development of structurally marginate petiole scales with dark apical setae, as noted in the key, but also in characters of their sporangia and spores. Although a discussion of the sporangia and spores of the entire family will be presented elsewhere, the bearing of these characters on the generic affinities of *Nephelea* merits brief consideration here. A survey begun by the author during this study of *Nephelea* indicates that, whereas sporangia containing sixty-four spores characterize the other genera of the family, *Nephelea* and *Alsophila* are characterized by the presence of sixteen-spored sporangia (Fig. 12). This diminished spore output appears to result from an abbreviated sporogenetic process whereby two of the four mitotic cell divisions typically preceding meiosis in sixty-four spored sporangia are absent. A survey of cyatheaceous spore morphology indicates that *Nephelea* and *Alsophila* are further characterized by a distinctive form of perine (Figs. 13–15). Although *Nephelea* cannot be separated from *Alsophila* on the basis of this perine morphology, both genera may be distinguished from the other genera in the family by this character.

Further evidence of the phyletic affinity of *Nephelea* and *Alsophila* is found in the appendages of their petiole bases and in their common potential for developing squaminate spines. Tryon has noted (1970, p. 28) that within the Cyatheaceae only *Alsophila* features fully developed aphlebiae at the base of the petiole. *Nephelea* exhibits a modified form of this character in *N. pubescens, N. setosa,* and *N. Grevilleana,* species characterized by leaves with subaphlebioid basal pinnae (Fig. 61). These are structurally intermediate between the highly dissected or filiform aphlebiae of many species of *Alsophila* and the normal basal pinnae of other species of

MAP 1. The distribution of Nephelea.

Nephelea. As indicated in the key above, *Nephelea* is characterized by the presence of conspicuous squaminate spines on the petioles and unexpanded croziers. The tendency of *Alsophila* to develop indurated and even squaminate spine-like petiole scales has been recognized by Tryon (1970, pp. 27–28), particularly in certain Madagascan and Antillean species. The full development of squaminate spines in *Nephelea* may be considered the ultimate expression of the potential or tendency seen in *Alsophila*.

The sporogenetic pattern, spore morphology, basal-pinnae structure, and potential for squaminate spine development, in addition to the characters of the petiole scales cited by Tryon, may therefore be taken to demonstrate the close phyletic relationship between *Nephelea* and *Alsophila* and to substantiate the expression of that relationship in his phyletic chart (Fig. 18, from Tryon, 1970, p. 12).

The close relationship between these genera and certain morphological patterns within *Nephelea* raise the issue of the degree of monophylesis of *Nephelea*. The uncommon pinnate-pinnatifid to pinnate-pinnatisect lamina

complexity and essentially cyathiform indusial morphology of *N. pubescens* and *N. balanocarpa* and the sub-aphlebioid basal pinnae of the former suggest a close affinity between these species and the pinnate-pinnatifid Antillean species of *Alsophila*. From an ancestral plexus similar to these two species, divergent geographic speciation may have given rise to the other species of *Nephelea*, which are characterized by a more dissected lamina. Such a derivation of *N. setosa*, however, may be particularly questioned. In its bipinnate-pinnatifid to tripinnate lamina, *N. setosa* resembles other species of *Nephelea*, but it is strongly characterized by sub-aphlebioid basal pinnae and is unique in the genus with a hemitelioid indusium. Its sub-aphlebioid basal pinnae may have been retained more or less unchanged from the condition of the ancestral complex while its lamina complexity increased and its indusial structure changed greatly, or these characters may reflect an independent close affinity of *N. setosa* to species of *Alsophila* with aphlebiae and hemitelioid indusia (for example *A. capensis*). If several independent origins of *Nephelea* from *Alsophila* did occur, *Nephelea* would still be considered monophyletic inasmuch as it was derived from a taxon of equal or lower rank (Simpson, 1961, p. 124). The issue cannot be discussed further with certainty until the infrageneric taxonomy of *Alsophila* is clarified by a revision of that genus.

Species and Speciation

I recognize only twenty-three of the fifty-nine taxa that have been formally proposed within the circumscription of *Nephelea*. The previous proposal of an excessive number of taxa was occasionally due to inadequate study but probably more often was the result of fragmentary early collections, few of which consisted of more than a single pinna or pinna-portion. Due to this, early authors could not know the range of variation in a taxon and could easily recognize minor variants as species. Because *Nephelea* was only recently recognized as a natural assemblage, comparisons of putative new species were often made with unrelated taxa, which served to enhance their distinctness. Finally, the biology of populations was not always appreciated and the species concepts of earlier authors, such as Hermann Christ, were strongly typological. Several early collectors, for example Wercklé in Costa Rica, were nurserymen with an eye for the unusual or even the aberrant, and the morphological extremes represented in some of their collections were quickly recognized as distinct new species.

The biological species concept and evolutionary principles have guided the assessment of taxa in this study, and have conferred an evolutionary dimension on what might otherwise have been a simple cataloging of morphological types. The determination of taxonomic rank has been inferential, based largely on evidence from morphology, geography, and ecology. Specific rank expresses the probability that the members belong

to the same actually or potentially interbreeding population or group of populations. Infraspecific rank indicates a lack of that degree of morphological divergence which is achieved in the species in this genus.

Geographic speciation (involving the geographic separation of elements of a species) has probably been largely responsible for the taxonomic diversity within *Nephelea*. This conclusion is based on the geographically correlated morphological variation observed in some taxa and the apparent lack of amphiploidy in the scaly genera (Tryon, 1970). As outlying populations migrate into areas at progressively greater environmental variance from that of the central population, the adaptive shift in gene frequencies may be reflected phenotypically. Given later isolation, differential selection pressure, and sufficient time, such populational divergence may proceed to speciation or to any of the taxonomically recognized infraspecific ranks.

Taxa which are morphologically distinctive and which have substantial allopatric ranges have been inferred to represent taxa at the rank of species, as two species pairs *Nephelea cuspidata* and *N. Sternbergii* (Maps 19, 20–21) and *N. Grevilleana* and *N. crassa* (Maps 4, 5). The approximation of other taxa to the rank of species has been inferred from their evolutionary performance in terms of morphological distinctiveness and geographic range relative to these species pairs.

Although the species of *Nephelea* have not been extensively investigated cytologically, there is reason to believe that ploidal differences have not been a significant factor in speciation. Walker (1966) reported cytological analyses of *N. Grevilleana*, *N. pubescens*, and *N. Tussacii* (as species of *Cyathea*). They have chromosome numbers of n=69 or $2n$=138, which are the numbers uniformly reported for every investigated species of the six squamate genera in the family (Tryon, 1970).

Morphology and Anatomy

Stem. The stem in all species is erect. The maximum heights attained by the different species are unknown, but the maximum recorded height in the genus is 15 m. in *Nephelea cuspidata* and *N. Sternbergii*. Under appropriate conditions, all species may develop a sheath of adventitious roots toward the base of the stem. Lucansky (1971, p. 53) has determined in *N. polystichoides* and *N. erinacea* var. *erinacea* (as *N. aureonitens*) that these roots arise both from the leaf bases and from the stem. The functional efficiency of these adventitious roots in a water-absorbing capacity is unknown, but they certainly add rigidity to taller stems and are their only means of radial growth. The greatest recorded stem diameter, including the adventitious root sheath, is 45 cm. in *N. Imrayana* var. *basilaris* from Estado Bolivar, Venezuela. The stem is dictyostelic with varying numbers of amphicribral meristeles, each surrounded by a dark sclerenchyma sheath. These, together with a hypodermal sclerenchyma sheath and the frequently developed adventitious root sheath, provide the major

mechanical support of the stem. Medullary and cortical bundles are present (Fig. 19), but on the basis of Central American material examined in cross section, these accessory bundles appear to be less numerous in *Nephelea* than in the other squamate genera. A thorough discussion of the arrangement and fate of the medullary and cortical bundles is provided by Lucansky (1971, pp. 54–66).

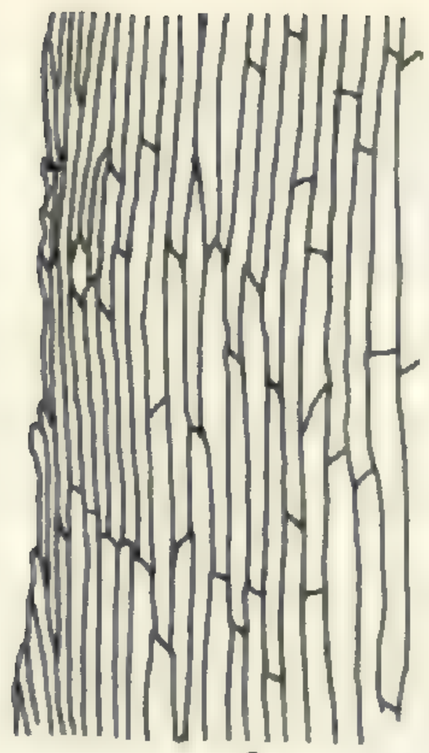
The leaves are disposed in vertical orthostichies and several vertical parastichies, or the spirals may be compressed and the internodes elongated so that the leaves are borne in whorls or apparent whorls. In *Nephelea erinacea*, *N. mexicana*, and *N. polystichoides*, I have frequently observed whorls of four leaves which give the stem a squarish cross section (Figs. 19, 20). Four to fifteen leaves per crown have been recorded in collections and their development may be sequential or apparently simultaneous in flushes.

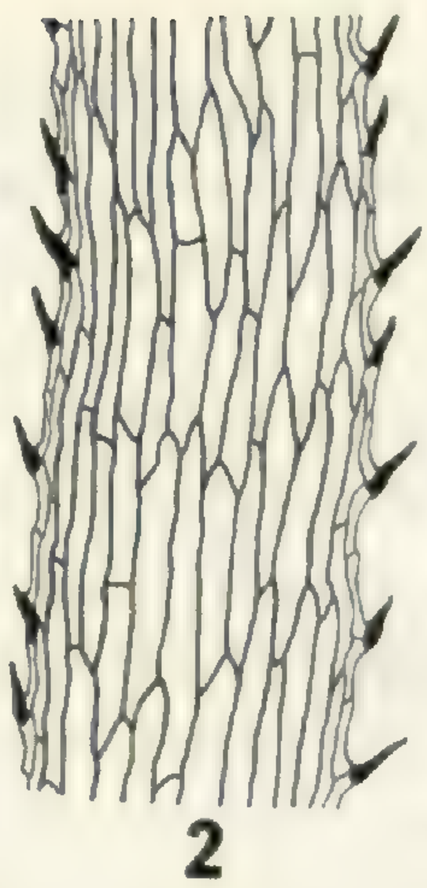
All species in which stem specimens have been seen bear persistent blackish spines on the stem (Fig. 23). Scales also invest the stem and may be best observed toward the apex, since they are eventually eroded below. The persistence and gradual erosion of dead leaf bases or their rapid and clean abscission is not consistent within a species, and I have been unable to determine environmental correlations. Adventitious buds have been observed in several species as well as lateral branching. Most specimens in this condition which I have personally observed had either been injured (see discussion below under *Nephelea woodwardioides* var. *Hieronymi*) or were growing in a disturbed habitat. In *N. polystichoides*, Lucansky (1971, pp. 53, 64) determined that adventitious buds arise on the latero-adaxial surface of the leaf bases and that the vascular supply to the bud is continuous with an adaxial leaf trace. I have observed positively geotropic buds on the stem of a plant of *N. mexicana* (Gastony & Gastony 993 [GH]) which was growing in an apparently undisturbed habitat. Vegetative reproduction by stolons has been reported by Brade (1971) in *Cyathea Sampaioana*. This is discussed below under *N. Sternbergii* var. *acanthomelas*.

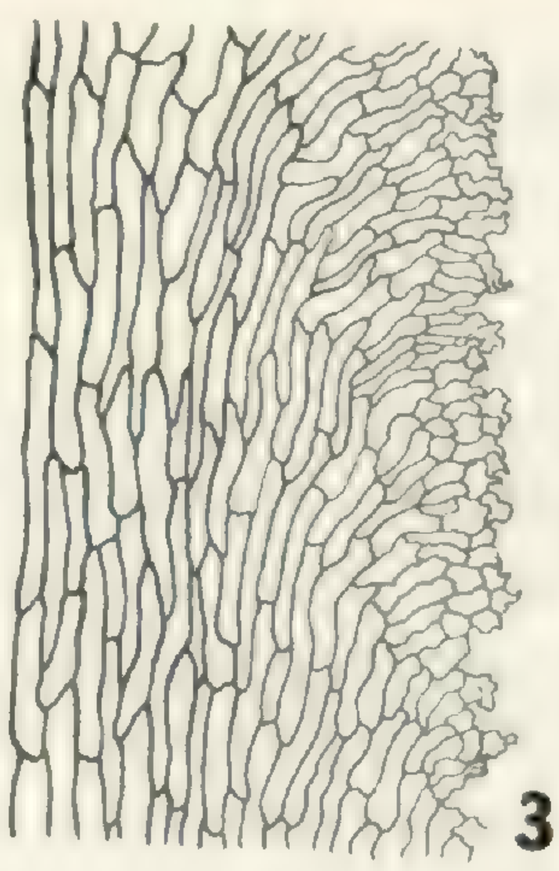
Leaf. Definitions of terms for the parts of the leaf are those of Tryon (1960).

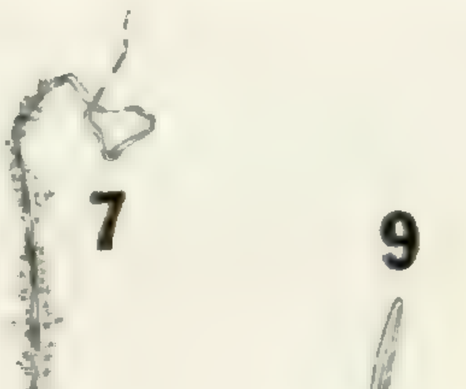
Petiole. The spines of the petiole provide one of the most useful generic characters, and the petiole indument is often diagnostic at the level of the species or species group. The petioles of all species are clearly characterized by the presence of blackish spines (Figs. 6, 16, 17). The phyletic derivation of these spines from typical *Nephelea* scales by multiplication and induration of the cells of the scale body (Figs. 7–9) has been discussed by Tryon (1970, p. 38). I am in complete agreement with his interpretation.

Although the scales on the adaxial surface at the base of the petiole are often more persistent than those on the abaxial surface, their margins









FIGS. 1–11. Petiole scale and spine characters of the squamate genera of the Cyatheaceae. FIGS. 1, 2. Portions of petiole scales of Sphaeropteris, representing the structurally conform condition, × 30:1, S. mollicula, *Schultes & Cabrera 13368a* (GH); 2, S. concinna, *Brass 3724* (GH). FIGS. 3, 4. Portions of petiole scales representing the structurally marginate condition, × 30:3, Alsophila Salvinii, *Hernandez* ×-*336* (US); 4, Cnemidaria spectabilis, *Britton et al. 1238* (NY). FIG. 5. Corticinate petiole spine bearing a peltate scale, Alsophila Manniana, *Goodwin 5* (GH), × 4. FIG. 6. Unexpanded crozier of Nephelea polystichoides, *Gastony & Gastony 793* (GH), × 1, the apical portion is the unexpanded crozier proper with spines among the scales, the basal portion has been detached from the stem and shows spines typical of the stem and petiole base. FIGS. 7–9. Transitions from petiole scales to squaminate spines, Nephelea erinacea var. erinacea, *Gastony & Gastony 763* (GH), all × 8; 7, Petiole scale thickened basally; 8, Spine-like petiole scale; 9, Small squaminate spine. FIGS. 10, 11. Petiole scale apices representing the rounded filamentous condition, × 90; 10, Cyathea parvula, *Proctor 5513* (GH); 11, Trichipteris mexicana, *Yuncker et al. 6015* (GH).

are usually poorly developed. Those on the abaxial surface are more varied in structural detail and provide substantial diagnostic utility at the species level. All of these scales are structurally marginate and feature a dark seta at the apex, the maximum length of which is, to some extent, correlated with species groups. The petiole scales of most Antillean species tend to be uniformly brown with the apical setae measuring a maximum of 0.1–0.25 mm. long, whereas the scales of continental species tend to be more delicate, with lighter colored margins and apical setae often reaching a length of 0.5–2.0 mm. The petiole scales of Antillean species and of several of the continental species lack dark setae other than at the apex (Fig. 66), whereas some continental species often, or in some cases consistently, bear additional smaller dark apical and lateral setae (Fig. 79). Besides these scales, which are often 20 mm. long and 1 mm. wide or larger, and occasional minute trichomidia, the petiole bears minute squamules which frequently are also dark-setate and grade in size into the larger scales.

In their spines and indument, there is no clear demarcation between petiole and rachis. In all species where I have seen adequate material, the petiole spines gradually diminish in size along the rachis.

Lamina. The complexity of the lamina division in *Nephelea* ranges from predominantly pinnate-pinnatifid (as in *N. pubescens*) to predominantly tripinnate-pinnatifid (as in some plants of *N. polystichoides*). In most species, lamina complexity varies between the base and apex of the pinnae. The most basal ultimate segments of basal pinnules are often one degree of complexity greater than more distal ultimate segments or those on more distal pinnules. For this reason, the lamina complexity in the species descriptions is given both as the maximum degree commonly found in the species and as the predominant degree exclusive of the most proximal and distal portions of the primary and secondary segments.

A strong dimorphism between sterile and fertile leaves does not characterize *Nephelea*. Most fertile and sterile leaves are practically monomorphic, and where a slight dimorphism has been observed, it is discussed under the species involved. The texture of the lamina varies from papyraceous to strongly coriaceous, usually with a narrow range of variation.

The form of the apex of the lamina, often poorly represented in herbarium collections, is generally correlated with the length of the apical seta of the petiole scale and serves to reinforce the distinction between the Antillean and continental species groups. The Antillan species generally have a gradually acute lamina apex (Fig. 21), whereas in the continental species the lamina is abruptly reduced to a distinct pinna-like apex (Fig. 22). Although the continental *Nephelea Tryoniana* is more or less intermediate between the two groups in the length of the apical setae of its petiole scales, the feature of a tapering lamina apex clearly places it with the Antillean species. The more or less abruptly reduced pinna-like lamina apex of the Lesser Antillean elements of *N. Imrayana* clearly associates them with the several continental species and supports the interpretation

of their derivation from South America. Further geographic implications are discussed under these species.

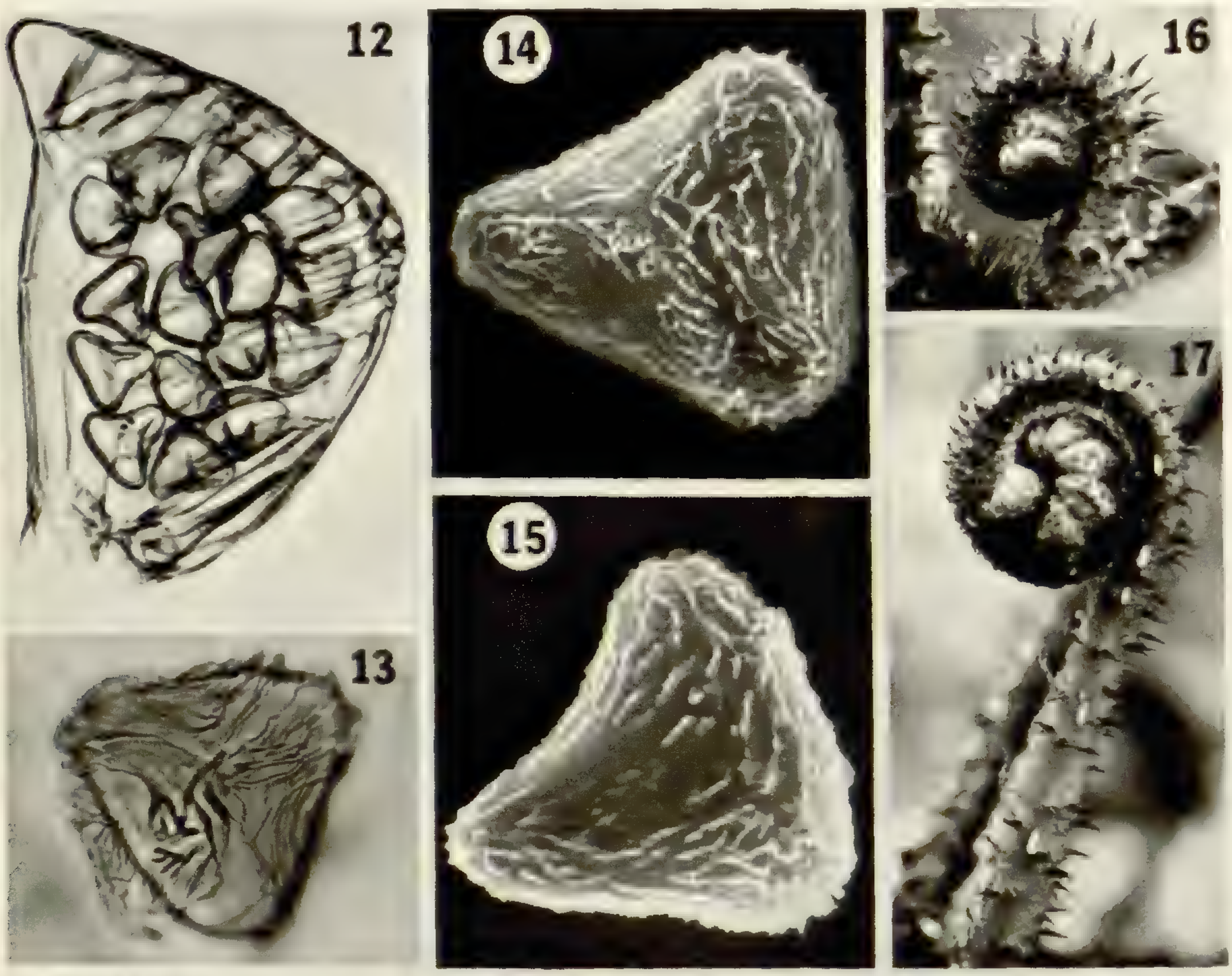
In describing the indument of the non-vascular lamina surface, the extremely minute and usually two-celled trichomidia which are commonly encountered in fern leaves have been disregarded. These are present, although often obscurely so, in all material examined. Except when their color takes on a more white or claret cast (usually randomly, but see the discussion under *N. Sternbergii* var. *acanthomelas*), they are inconspicuous even at magnifications of sixty diameters.

Venation. The venation in all species is free, never reticulate. In most species the veins are predominantly once-forked, but are mostly simple in *Nephelea concinna* and in the most complex forms of *N. polystichoides* where they are borne on quintary axes. The venation pattern and the extent of lamina surface are correlated, although this was not recognized by some early taxonomists. In small or narrow ultimate segments, the veins are commonly simple as they also are toward the distal ends of larger segments. As the surface area of ultimate segments increases, the simple veins do not increase in number; they fork or branch instead. As ultimate segments approach a lobed condition, the venation becomes increasingly branched, or finally a midvein and simple laterals develop in large lobes. The veins of an ultimate segment are commonly branched proximally in the segment, once-forked medially, and simple distally. The primary forking is usually at or near the costule, but as the zone of simple veins is approached distally in the segment, the forking tends to occur farther from the costule. The descriptions of venation in the species treatments refer to the predominant condition more or less medially in the ultimate segments.

The indument on the abaxial surface of the costa, costule, and veins is of particular diagnostic value; a diminutive form of the indument on the axis of one order of branching is often present on the axis of the next higher order. As squamules on these axes become progressively smaller, their morphology occasionally grades into that of trichomes, through trichomes which are uniseriate at the base and biseriate or multiseriate above. Such transitions suggest the phyletic derivation of the squamules from trichomes. In other instances the smallest squamules appear more or less stellate with various kinds of processes. As these approach the condition of trichomes, it is diagnostically very useful to distinguish the various forms which are found to be species specific. For this reason, the stellate trichomes of *Nephelea cuspidata* (Fig. 80), the stellate squamules of *N. erinacea* (Fig. 67), and the highly trichomoid stellate squamules of *N. Sternbergii* var. *Sternbergii* (Fig. 84) have been illustrated.

Sorus and Associated Structures. Structures associated with the sorus provide very useful diagnostic characters, but they show as much variation as other aspects of the species morphology. Variability in these structures is to be expected in any outbreeding diploid population.

Nephelea Tryoniana is the only species in the genus which is truly exindusiate. In *N. setosa* (Fig. 60), the indusia are hemitelioid, well-developed and attached to only one side of the receptacle. In all other species in the genus the indusia are attached completely around the base of the receptacle. In the latter case, the indusia may enclose the sori to varying degrees. Tryon (1970, p. 8) recognized such indusia as cyatheoid if they are open at the apex and as sphaeropteroid if they are closed at the apex. For purposes of greater refinement, I have recognized three subtypes of the cyatheoid indusium—meniscoid, cyathiform, and urceolate—and I have recognized a variant of sphaeropteroid as sub-sphaeropteroid. Meniscoid indusia are shaped like a concave meniscus or watch-glass; cyathiform indusia are cup-shaped and a little wider at the top than at the bottom (Fig. 52); urceolate indusia are pitcher-like with the mouth more or less contracted; sphaeropteroid indusia completely enclose the sorus



FIGS. 12–17. Nephelea sporangium, spores, and croziers. FIG. 12. Sporangium of N. woodwardioides var. woodwardioides, cleared in sodium hydroxide to show its contents of sixteen spores. View is through stomial side of capsule, *Maxon 4035* (F) × 200. FIG. 13. Acetolysed spore of N. woodwardioides var. cubensis, the perine fragmented in the acetolysis process and beginning to separate from the psilate exine, *Wright 948*, (GH) × 500. FIGS. 14, 15. Scanning electron micrographs of N. cuspidata spores entirely covered with an irregularly ridged or striate perine, *Krukoff 10841*, (GH) × 900: 14, Proximal surface; 15, Distal surface. FIGS. 16, 17. Croziers of young sporophytes of N. Tussacii showing well-developed squaminate spines representative of Nephelea in general, both × ca. 0.5. Some of these spines are caducous with crozier expansion, the majority persist as the spines of the petiole in the mature leaf: 16, Young crozier beginning expansion, *Gastony & Gastony 1025* (GH); 17, Expanding crozier showing spines of part of the petiole as well as of the still unexpanded crozier portion, *Gastony & Gastony 1026* (GH).

and are closed at the apex where they often feature an umbo (Fig. 74). In sub-sphaeropteroid indusia, the apex is barely or not quite closed. These are degrees of development convenient for descriptive purposes and are often quite discrete in a given species although intergrading conditions can be found.

The texture of the indusium may be quite firm, in which case it remains entire and persistent if meniscoid to cyathiform or else ruptures, but is usually persistent, if urceolate to sphaeropteroid. When its texture is delicate, the indusium is easily ruptured by the expansion of the sorus, as when the sporangia open at maturity, or upon drying. In proportion to their delicacy, such indusia are usually partially or almost completely fugacious, as in *Nephelea mexicana*, *N. polystichoides*, and *N. Sternbergii* var. *acanthomelas*. Careful examination reveals the presence of indusial remnants at the base of the receptacle in material of this nature, but these remnants were occasionally overlooked by some early authors who placed such specimens in the classical genus *Alsophila*. The indusia may be glabrous or variously pubescent, and the pubescence is usually a diminutive form of that found abaxially on the veins.

The species of the Greater Antilles are characterized by meniscoid to cyathiform indusia of firm texture. With the exception of *Nephelea incana* and *N. Sternbergii* var. *Sternbergii*, the indusia of the continental species are more delicate or more enclosing than those of the Greater Antilles.

In all species, the sporangia are borne on a receptacle which is situated

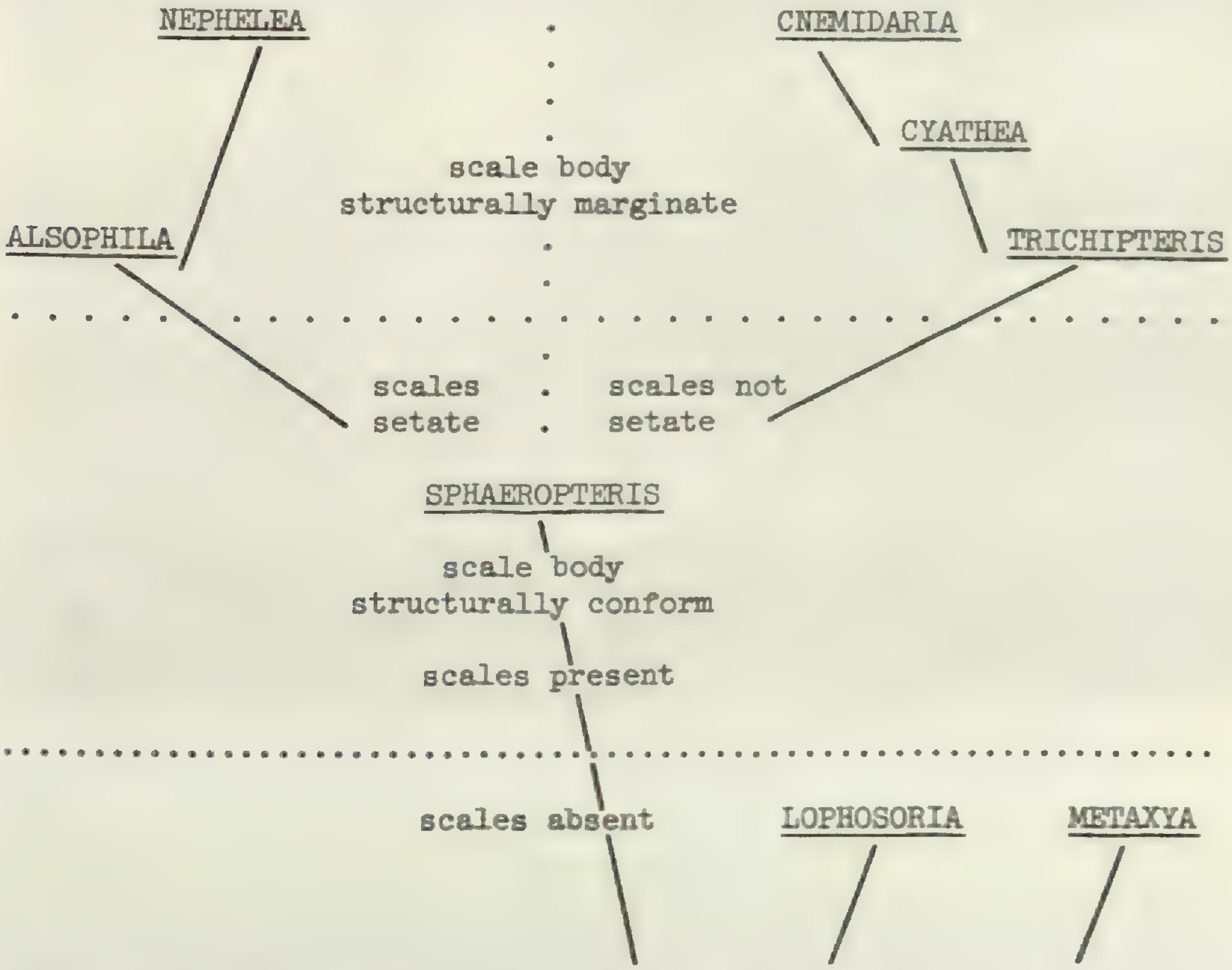
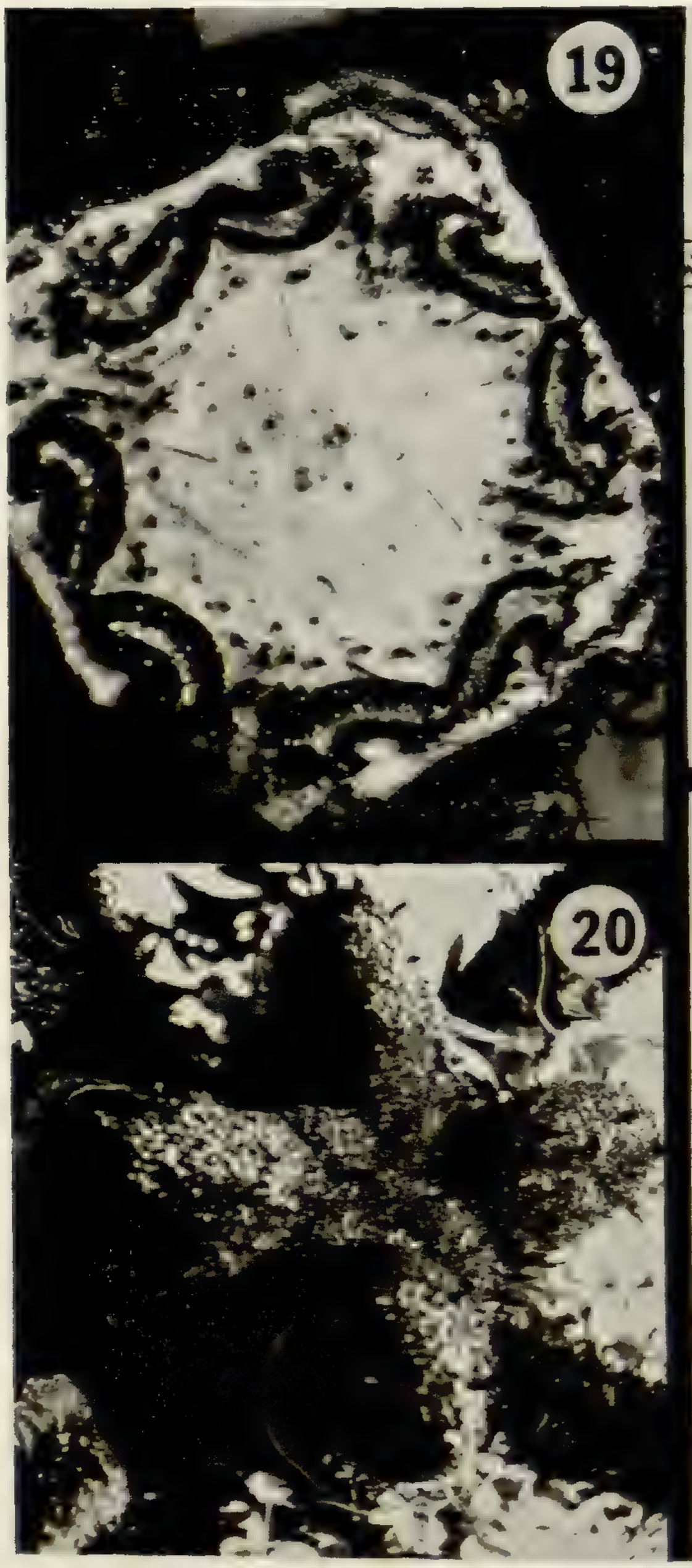
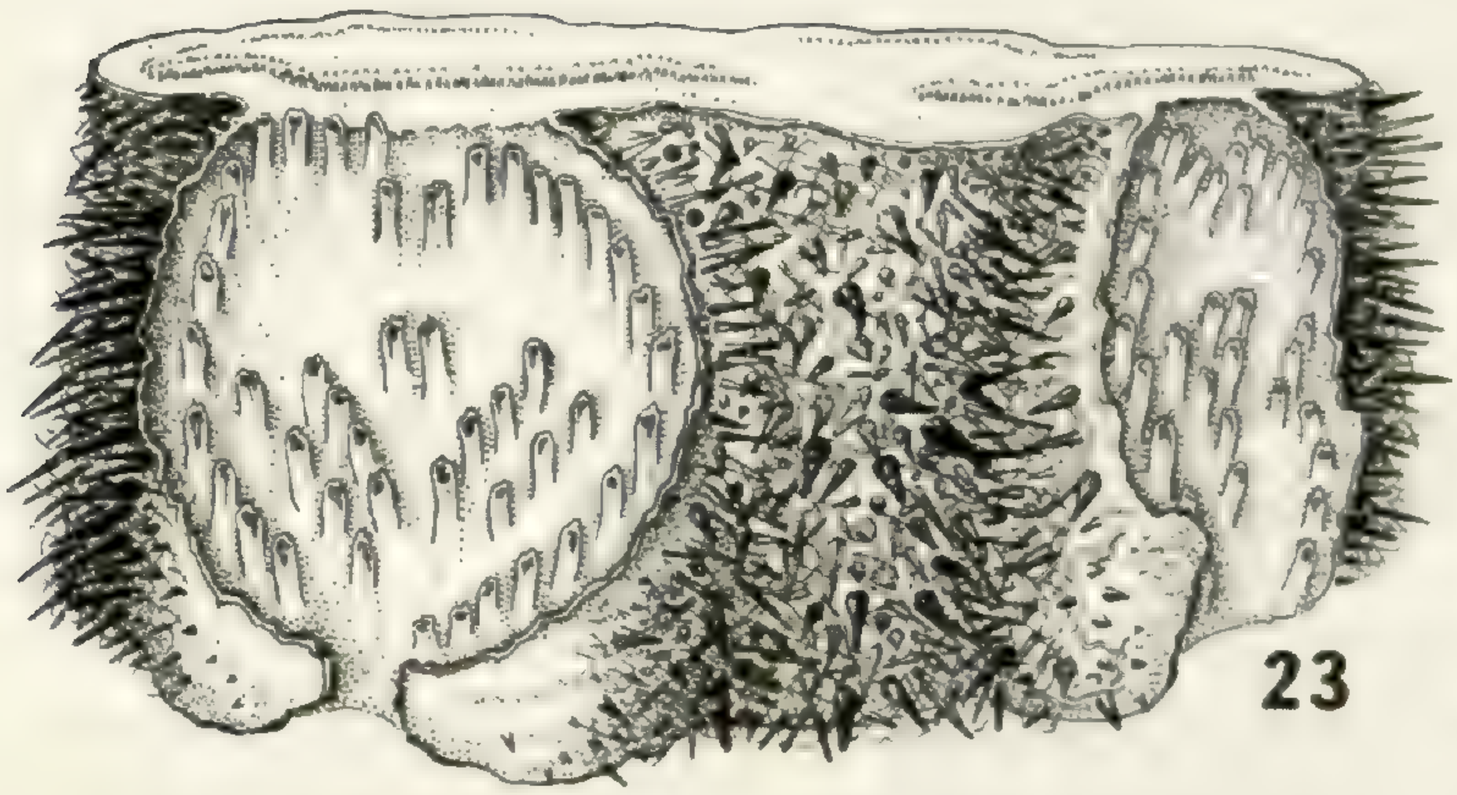


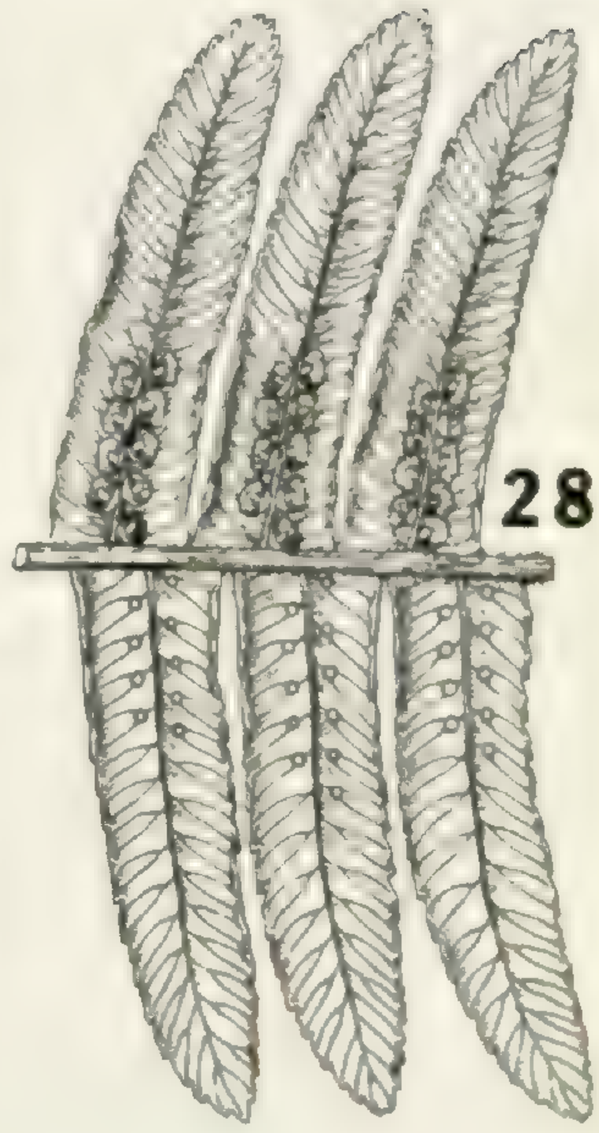
FIG. 18. Phyletic chart of the Cyatheaceae (from Tryon, 1970, p. 12).

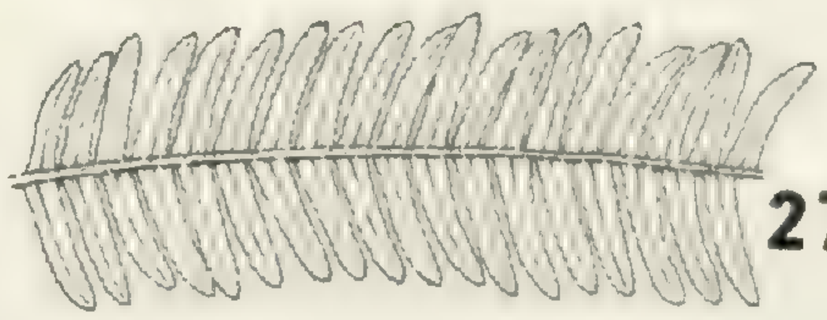
at the primary forking of the veins or at or near the costule on simple veins. The shape of the receptacle is columnar or more or less globose on a very short stalk (Figs. 52, 60). In most species the form varies between these conditions but in some, the columnar (as in *Nephelea crassa*) or the globose form (as in *N. cuspidata*) may be constant or nearly so. For descriptive purposes, the receptacle is termed exserted when it extends



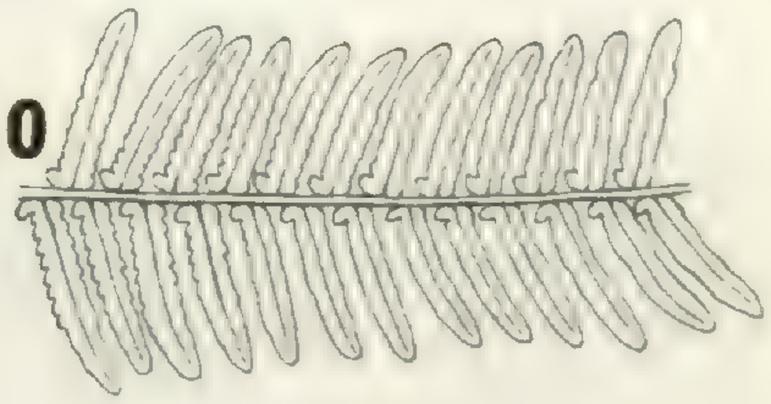
FIGS. 19–22. Stem, apex, and leaf apices of Nephelea. FIG. 19. Cross section of a stem of N. polystichoides as in Fig. 20. Note the squarish shape of the section, the dark sclerenchyma sheath around each meristele, and the relatively few medullary and cortical bundles, *Tryon & Tryon 6990* (GH), × ca. 0.6. FIG. 20. Stem apex of N. polystichoides. Note the four unexpanded spiny croziers subtended by four alternate petioles, the petioles and croziers each in an apparent whorl, *Tryon & Tyron 7021* (GH), reduced. FIGS. 21, 22. Apical portions of leaves of Nephelea, reduced: 21, Gradually acute apex of N. crassa, representing the lamina apex condition of the Antillean species of Nephelea, *Gastony et al. 647* (GH); 22, Abruptly reduced pinna-like apex of N. mexicana, representing the lamina apex condition of the continental species of Nephelea, *Gastony & Gastony 751* (GH).

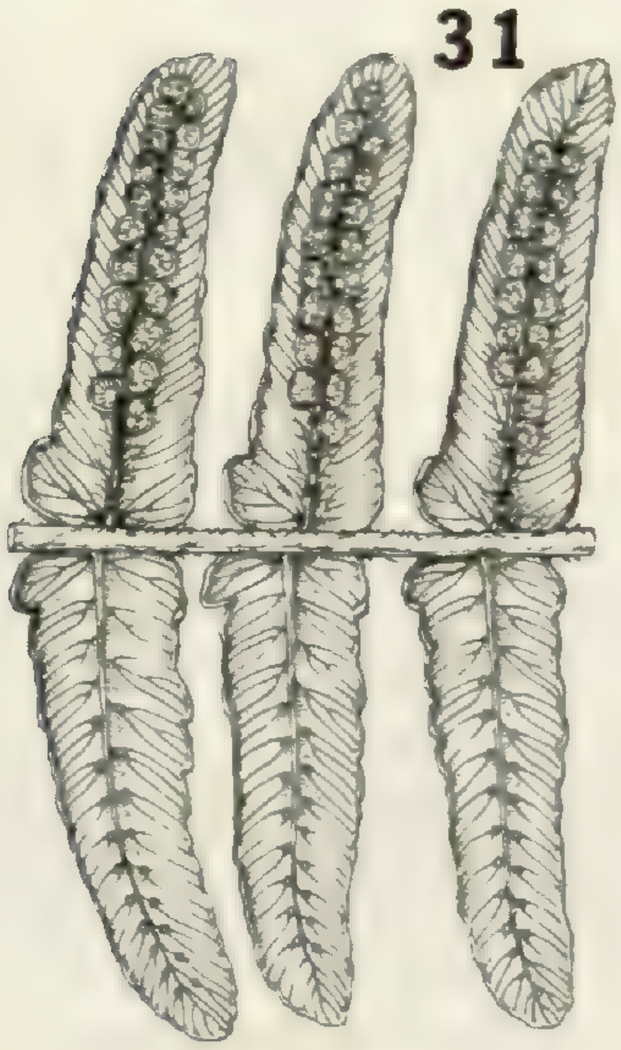


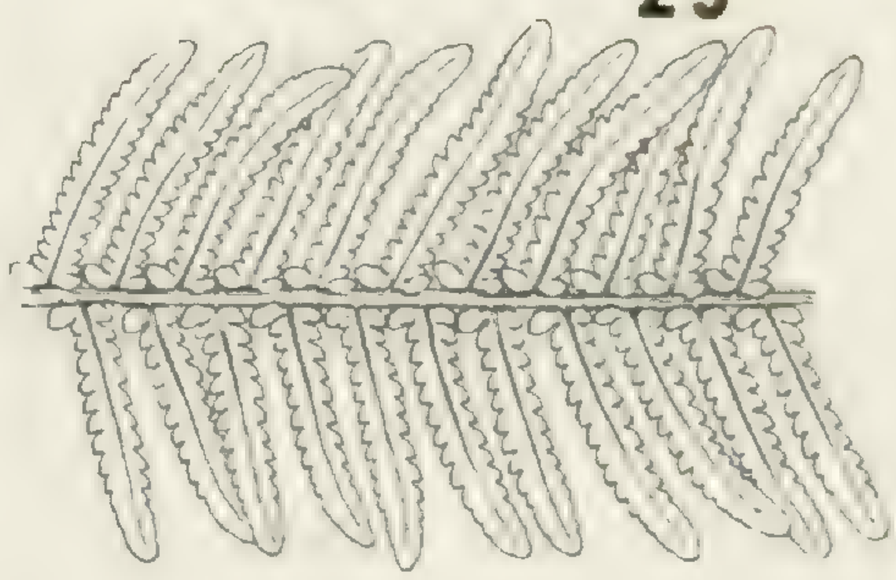




100 μ







FIGS. 23–26. Nephelea stem portion and sporangia. FIG. 23. Portion of a stem of N. erinacea var. erinacea bearing scales and persistent blackish squaminate spines between the leaf scars, *Gastony & Gastony 763* (GH), × 1. FIGS. 24–26. Three views of representative Nephelea sporangia, N. woodwardioides var. Hieronymi, *Gastony et al. 156* (GH), all × 140. Note the complete, oblique, uninterrupted annulus which gives the sporangium a hooded appearance; one tier of the four stalk cells is shown attached to the face cells. Note in Figs. 24 and 26 that the stomial region may occur on either side of the annulus. FIGS. 27, 28. Nephelea pubescens, *Crosby et al. 312* (F): 27, Central portion of a central pinna, × 0.5; 28, Central pinnule-segments of a central pinna, × 2. FIGS. 29–31. Nephelea balanocarpa: 29, Central pinnules of a central pinna, *Wright 1063* (GH), × 0.5; 30, Central and sub-central pinnules and pinnule-segments of a central pinna, *Maxon 4031* (GH), × 0.5; 31, Central pinnule-segments of a central pinna, *Maxon 4031* (GH), × 2.

beyond the mouth of the indusium and inserted when it does not. The receptacle occasionally splits longitudinally when dried, but I am unable to assign this any taxonomic significance as Presl did [sic, 1836] in describing his genus *Disphenia*.

The paraphyses in *Nephelea* are quite short and inconspicuous, reaching a maximum length of 0.1–0.4 mm., unlike those of *Sphaeropteris*, *Trichipteris*, and *Cyathea* which are often much longer and more conspicuous. As in the case of the receptacle, the paraphyses are termed exserted when they extend beyond the mouth of the indusium and inserted when they do not. They are commonly uniseriate but occasionally may be biseriate or multiseriate and squamuloid. In the latter case, as discussed under *N. Grevilleana*, they are relatively conspicuous, especially at the apex of the receptacle, and their morphology often suggests their derivation from abortive sporangia.

The sporangia (Figs. 24–26) are small, with a stalk of four rows, each one, or at the most two, cells long, and each contains only sixteen spores (Fig. 12). The complete, oblique annulus has a lateral stomium on either side of the capsule (Figs. 24 and 26) and is uninterrupted by the stalk.

The tetrahedral-globose spores are produced in tetrads and are covered by a perine which provides their only distinctive morphology as the exine is psilate. The perine develops irregular ridges both in *Nephelea* (Figs. 13–15) and in the closly related genus *Alsophila*. Although *Nephelea* cannot be separated from *Alsophila* on the basis of the perine morphology, both may be distinguished from other genera in the family by this character. Spore morphology is, therefore, of limited value as a generic character of *Nephelea* but is of no demonstrated value in distinguishing its species.

ACKNOWLEDGMENTS

This paper is based on a Ph.D. dissertation of the same title presented to the Department of Biology, Harvard University. I am particularly grateful to Dr. Rolla M. Tryon of the Gray Herbarium for his unfailing advice and encouragement throughout this study and to Dr. Alice F. Tryon for instructive discussions, advice, and assistance. I thank Professor Elso S. Barghoorn for the use of the equipment and facilities of the Paleobotanical Laboratories and Professor Reed C. Rollins, Director of the Gray Herbarium, for his constant support. For the illustrative drawings I am indebted to Lydia V. Wunsch.

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Special acknowledgment is given to Dr. Rolla M. Tryon for the use of notes made during his European study of type specimens of the Cyatheaceae. References in the text to Rolla Tryon in 1969 are to these notes. I am further indebted to Dr. Tryon for the use of the illustrations in Figs. 1–11, 18, and 23.

This study has involved the examination of some 2,300 herbarium sheets. The abbreviations of herbarium citations are those standardized by Lanjouw and Stafleu (1964). I am grateful to the officers of the following herbaria for the use or loan of materials: A, B, BM, BR, C, DUKE, F, GH, HB, IJ, K, LE, LIL, M, MO, NY, P, PRC, R, S, S-PA, SP, TRIN, UC, US, YU.

I am indebted to Jeol, Inc., Medford, Massachusetts for the use of their JSM-2 scanning electron microscope. Genus and species ranges have been plotted on the Goode Series of base maps, published by the University of Chicago Press, Chicago, Illinois.

SYSTEMATIC TREATMENT

1654

Nephelea Tryon, Contrib. Gray Herb. 200: 37. 1970. TYPE SPECIES: *Nephelea polystichoides* (Christ) Tryon, (*Cyathea polystichoides* Christ).

Cyathea pro parte, auct. pl., e.g., Maxon, North Amer. Fl. 16: 65–88. 1909.

Hemitelia pro parte, auct. pl., e.g., Mettenius, Fil. Lechl. 2: 30. 1859.

Alsophila pro parte, auct. pl., e.g., Christ, Bull. Herb. Boiss. II, 4: 957. 1904.

Lophosoria pro parte, Fée Crypt. Vasc. Brésil 1: 173. 1869.

Stem dictyostelic with medullary and cortical bundles, erect, to 15 m. tall and 45 cm. in diameter including the investing sheath of adventitious roots, bearing scales especially toward the apex and blackish spines to 5–26 mm. long, occasionally with adventitious buds. *Unexpanded croziers* lacking trichomes, densely squamose, and with blackish squaminate spines to 5–17 mm. long, many of them caducous with the expansion of the crozier. *Petiole* with blackish obturbinate to conical, squaminate spines to 4–15 mm. long, the scales on the abaxial surface patent, fully adnate or slightly narrowed at the base, structurally marginate, with a narrow to broad margin of cells different in orientation, size, shape, and usually in color from those of the central portion, bearing a dark apical seta to 0.25–2.0 mm. long and occasionally additional smaller apical and lateral setae, minute indument, when present, of trichomidia and/or of squamulae. *Lamina* to 1.7–3.5 m. long and 0.7–2.0 m. wide; *costa* pubescent adaxially; *veins* free, simple or forked at or near the costule, in lobed or pinnatifid segments, the basal vein on each side extending above the base of the sinus; *sori* at or near the costule, at the fork of the vein or on simple veins, *indusium* lacking or present and hemitelioid or meniscoid to sphaeropteroid, *sporangia* numerous, borne on a nearly globose to columnar receptacle, each containing 16 spores and with an oblique, uninterrupted annulus, *paraphyses* short (to ca. 0.1–0.4 mm. long), mostly inconspicuous but occasionally tufted at the apex of the receptacle, *spores* tetrahedral-globose, brown at maturity, with a completely enclosing striate perine.

USE OF THE KEY

The degree of complexity of lamina division employed in the key is not the full range given in the species descriptions, but is determined (where applicable) beyond the basal segments of central pinnules of central pinnae. Because of their great diagnostic value, several minute and often obscure characters have been employed in the key. It is strongly recommended that specimens be examined with up to 60 × magnification.

KEY TO THE SPECIES OF NEPHELEA

A. Lamina pinnate-pinnatifid to bipinnate (based on central portions of central pinnae) ..... B.

B. Central pinnule-segments of central pinnae fully adnate or nearly so and lacking auricles, their margins serrate-dentate with the teeth mostly bifid, their apices strongly serrate-dentate; basal pinnae often sub-aphlebioid (Fig. 61). Jamaica ..... 1. *N. pubescens.*

B. Central pinnules or pinnule-segments of central pinnae sessile (not fully adnate) and usually auriculate especially on the basiscopic side, their margins entire-undulate to dentate-lobate with teeth simple when present, their apices entire to serrulate; basal pinnae reduced in size but not sub-aphlebioid. Cuba ..... 2. *N. balanocarpa.*

A. Lamina bipinnate-pinnatifid to tripinnate-pinnatifid (based on central portions of central pinnae) ..... C.

C. Indusia absent or hemitelioid ..... D.

D. Indusia absent; costae and costules abaxially with bullate scales (trichomes may also be present); basal pinnae reduced in size but not sub-aphlebioid. Guatemala, Honduras, Nicaragua ..... 11. *N. Tryoniana.*

D. Indusia hemitelioid (Fig. 60); costae and (or) costules abaxially with flattish scales (trichomes may also be present); basal pinnae sub-aphlebioid (Fig. 61). Brazil, Argentina, Paraguay ..... 10. *N. setosa.*

C. Indusia meniscoid to sphaeropteroid (sometimes rupturing at maturity, or upon drying, into segments, which may be fugacious leaving only a remnant at the receptacle base) ..... E.

E. Pinna-rachis not greenish-alate between the more distal sessile pinnules .... F.

F. Costa and (or) costule abaxially with bullate scales (Figs. 34, 35) trichomes present or absent, or these axes glabrescent ..... G.

G. Indusia sphaeropteroid to sub-sphaeropteroid, rupturing into 2–3 persistent segments with soral maturity; lamina very coriaceous; (at 15 × magnification the dried mature epidermal tissue reticulate adaxially and the stomatal apparatus conspicuous abaxially). Hispaniola ..... 5. *N. fulgens.*

G. Indusia cyathiform to urceolate, usually intact at soral maturity ..... H.

H. Costa abaxially with scales predominately bullate to sub-bullate (some flattish ones may be present); largest pinnules not exceeding 5.5 cm. long, usually much shorter; fertile pinnules often appear auriculate proximal to and abruptly pinnatifid distal to the usually more or less pinnatilobate fertile zone (Figs. 56, 57); veins mostly simple; (adjacent pinnules often quite unequal in length Fig. 53). Jamaica ..... 9. *N. concinna.*

H. Costa abaxially with scales predominantly flattish (some bullate ones may be present); largest pinnules usually exceed 5.5 cm. long; fertile pinnules not appearing auriculate, pinnatifid throughout; veins mostly branched ..... I.

I. Pinna-rachis abaxially more or less persistently squamose (the scales to ca. 5 mm. long, stramineous the larger ones often with a brown central stripe, sub-peltately attached to usually darkened epidermal emergences); costa abaxially densely squamose, the scales stramineous (or with a brown stripe), often with only a single dark apical seta. Jamaica .... 8. *N. Tussacii.*

I. Pinna-rachis abaxially not persistently squamose; costa abaxially not densely squamose or if so the scales mostly brown to blackish and frequently with more than one dark seta ..... J.

J. Basal pinnae usually sub-aphlebioid (as in Fig. 61); segment margins serrate-dentate; costa adaxially usually densely pubescent; costule abaxially with strongly bullate scales and stiff trichomes, adaxially usually with stiff trichomes. Jamaica ..... 3. *N. Grevilleana.*

J. Basal pinnae reduced in size but not sub-aphlebioid; segment margins entire or nearly so, or if serrate-dentate the costa adaxially sparsely pubescent to glabrescent; costule abaxially with strongly bullate to sub-bullate scales or the scales lacking, only rarely with stiff trichomes, adaxially lacking stiff trichomes ..... K.

K. Costule abaxially glabrous or glabrescent, or if with bullate scales and trichomes, the segment margins strongly serrate-dentate; lamina rigidly papyraceous; pinna-rachis adaxially usually sparsely pubescent. Hispaniola . . . . . 4. *N. crassa.*

K. Costule abaxially with numerous bullate to sub-bullate scales and often with stiff trichomes; segment margins entire to nearly serrate-dentate, or if serrate-dentate the costule abaxially lacking stiff trichomes; lamina rigidly papyraceous to coriaceous; pinna-rachis adaxially usually densely pubescent. Cuba, Jamaica, Hispaniola . . . . . 7. *N. woodwardioides.*

F. Costa and (or) costule abaxially with flattish scales, trichomes present or absent . . . . . L.

L. Veins, or some of them, abaxially with (sometimes few) minute, whitish stellate squamules with a variable number of irregular processes (Fig. 67), occasionally small dark-setate squamules as on the costule may also be present (petiole base abaxially with scales with a single dark apical seta and without dark lateral setae, Fig. 66). Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia. . . . . 12. *N. erinacea.*

L. Veins abaxially lacking indument or the indument not stellate . . . . . M.

M. Indusia cyathiform to urceolate, brownish, firm and usually intact at maturity, bearing more or less stiff trichomes; (occasionally some of the scales abaxially on the costule sub-bullate). Puerto Rico . 6. *N. portoricensis.*

M. Indusia sphaeropteroid to sub-sphaeropteroid, often partially to almost completely fugacious at maturity or when dried, not bearing trichomes. Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Trinidad, Venezuela, Colombia, Ecuador, Panama, Costa Rica . . . . . 13. *N. Imrayana.*

E. Pinna-rachis greenish-alate between the more distal sessile pinnules (more or less as in Fig. 94) . . . . . N.

N. Costa and (or) costule abaxially with bullate scales (Figs. 34, 35), trichomes present or absent, or these axes glabrescent. (Plants of species 3–5 with alate pinna-rachis—see headings G above.)

N. Costa and (or) costule abaxially with flattish scales, trichomes present or absent . . . . . O.

O. Veins, or some of them, abaxially with stellate trichomes or strongly trichomoid stellate squamules, occasionally small dark-setate squamules as on the costule may also be present . . . . . P.

P. The stellate trichomes often with 3–4 distinct more or less straight (sometimes dark) arms (Fig. 80); indusia mostly sub-sphaeropteroid, dark brown, firm, persistent, frequently splitting into 2–4 segments at maturity, usually bearing stellate trichomes similar to those on the veins; petiole base abaxially with scales with several dark apical setae and few to many dark lateral setae (Fig. 79). Nicaragua, Costa Rica, Panama, Colombia, French Guiana, Ecuador, Amazonas Brazil, Peru, Bolivia, Paraguay . . . . . 14. *N. cuspidata.*

P. The stellate trichomes or strongly trichomoid stellate squamules and the indusial characters variable; either the stellate vein indument conspicuous with long whitish irregular arms (Fig. 84) and the indusia brown, firm, and persistent with similar indument, *or* the stellate vein indument less conspicuous with less prominent arms and the indusia diaphanous to light brown, delicate and more or less fugacious, with similar indument or glabrescent; petiole base abaxially with scales with or without more than one dark apical seta and dark lateral setae. Brazil, Paraguay 15. *N. Sternbergii.*

O. Veins abaxially lacking indument or the indument not stellate . . . . . Q.

Q. Indusia meniscoid to shallowly or deeply cyathiform or sub-sphaeropteroid, the more sphaeropteroid ones ruptured but persistent at maturity, bearing soft, often crispate trichomes or trichomoid processes. Colombia, Ecuador, Peru, Bolivia, Argentina . . . . . 16. *N. incana.*

Q. Indusia sphaeropteroid to sub-sphaeropteroid, often partially to almost completely fugacious at maturity or when dried, not bearing trichomes or trichomoid processes . . . . . R.

R. Tertiary axes not alate between the tertiary segments; complexity of the lamina not more than bipinnate-pinnatifid. Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Ecuador .... 17. *N. mexicana.*
R. Tertiary axes alate between some or all of the tertiary segments (Figs. 95–98); complexity of the lamina bipinnate-pinnatifid to tripinnate-pinnatifid. Costa Rica, Panama ..... 18. *N. polystichoides.*

1. **Nephelea pubescens**

(Kuhn) Tryon, Contrib. Gray Herb. 200: 40. 1970.

FIGS. 27, 28, MAP 2

Cyathea pubescens Mett. ex Kuhn, Linnaea 36: 164. 1869. TYPE: Jamaica, collector not stated but probably 1843, *Purdie.* A portion of a leaf ("comm. Sir W. Hooker 1859") at B! in the hebarium of Mettenius and determined by him is certainly the holotype, fragments of this specimen are at B! in the herbarium of Kuhn; isotypes: BM! (two sheets).

Stem to 7 m. tall and 7 cm. in diameter, bearing brown scales especially toward the apex and blackish-brown spines to 11 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 11 mm. long and brown scales with a short (ca. 0.1 mm. long) dark apical seta and without lateral setae. *Petiole* to ca. 0.25 m. long, dark brown, with blackish spines to 9 mm. long, the scales on the abaxial surface more or less few, nearly uniformly brown with a dark apical seta to 0.1–0.2 mm. long and without lateral setae. *Lamina* subcoriaceous, to ca. 2 m. long and 0.7 m. wide, bipinnate-pinnatilobate to bipinnate-pinnatifid (predominately pinnate-pinnatifid), with a gradually acute apex. *Rachis* light brown, adaxially densely pubescent and more or less squamose, abaxially furfuraceous to glabrescent. *Central pinnae* sessile, narrowly elliptic-lanceolate to narrowly ovate-lanceolate, to 36 cm. long and 4.5 cm. wide; *basal pinnae* highly reduced, to ca. 7 cm. long and sub-aphlebioid in structure; *costa* (*pinna-costa*) adaxially pubescent with intermixed long narrow tan scales, abaxially furfuraceous to pubescent distally, lacking conspicuous pneumatodes at costule axils, not alate. *Pinnule-segments* to ca. 3.2 cm. long and 0.4 cm. wide, straight to sub-falcate with lateral margins serrate-dentate (the teeth mostly shallowly bifid, corresponding to the vein endings), apex serrate-dentate, margins flat to revolute, the more or less central pinnule-segments usually fully adnate to nearly so, basal pinnule-segments (pinnules) often pinnatilobate to pinnatifid and usually sessile to petiolulate; *costule* adaxially sparsely pubescent, abaxially stiffly pubescent and usually with occasional bullate to sub-bullate often dark-setate squamules 0.25–0.5 mm. long, scales not clustered in the axil; *veins* once-forked at or near the costule, evident on both surfaces, adaxially usually glabrous, rarely sparsely pubescent, abaxially glabrous or frequently with stiff trichomes; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the forking of the veins; *indusium* meniscoid to cyathiform (rarely urceolate), brown, of firm texture, persistent and entire at maturity, glabrous; *receptacle* columnar to globose, usually exserted, with inconspicuous, short (ca. 0.2–0.3 mm. long) paraphyses.

In 1969, Rolla Tryon noted at BM that a collection in the herbarium of Rawson "Jamaica, ded. Hooker 1859" corresponds in detail with collections of Purdie, Jamaica, 1843 in the herbarium of John Smith. He reasoned that the Purdie 1843 collection was probably the one distributed by Hooker and received by Mettenius, among others. I have studied a BM sheet of Purdie 1843 from the herbarium of John Smith together with the type and agree that they appear to be parts of the same collection. These sheets in the John Smith herbarium and in the Rawson herbarium at BM may therefore be taken as isotypes.

Nephelea pubescens is notable because of its sub-aphlebioid pinnae toward the base of the lamina. Such sub-skeletonized pinnae are uncommon in *Nephelea*, being found elsewhere only in *N. Grevilleana* and *N. setosa* (Fig. 61). Although the degree of skeletonization is somewhat variable in *N. pubescens*, the pinnules of these lower pinnae are nearly always more dissected than their counterparts on other pinnae.

Nephelea pubescens is endemic to the Blue Mountains of Jamaica at altitudes of 1250–2200 m., where it is common in wet, mossy forest, in ravines, and on moist, cloud forest slopes. Specimens commonly called by this name from Cuba, Hispaniola, and Puerto Rico lack spines on the petioles and croziers and belong to species of the genus *Alsophila*.

ADDITIONAL SPECIMENS EXAMINED: **Jamaica.** *Eggers 3638* (F,M); *Gilbert 80* (NY); *Jenman 44* (UC). **Portland:** *Gastony 23, 120* (GH); *Moore & Read 9557* (GH); *Orcutt 5142* (UC); *Proctor 4333* (MO); *Riba 233* (GH). **Portland-St. Thomas:** *Maxon 9669* (GH,M,NY,US); *Maxon & Killip 1712* (F,GH,NY,US). **St. Thomas:** *Hunnewell 14257* (GH); *Maxon 1432, 1446* (US), *9987* (GH,NY,US), *10138* (NY,US); *Proctor 4182* (US); *Underwood 2468, 2551* (NY). **St. Andrew:** *Crosby et al. 312* (F,MO,NY,UC,US); *Hespenheide et al. 1467* (GH); 1932, *Papenfuss* (UC); *Wilson 525* (A,US). **St. Andrew-Portland:** *Chrysler 4547* (MO); *Clute 90* (MO,NY,US); *Eggers 3635* (US); *Fisher 96* (NY); *Harris 7219* (NY), *7719* (F,NY,US); *Hatch 6* (US); *Johnson 4* (F); *Killip 287* (US); *Maxon & Killip 661* (F,GH,NY,US); *Underwood 1531* (NY,US), *1533* (NY).

2. Nephelea balanocarpa

(D. C. Eaton) Tryon, Contrib. Gray Herb. 200: 38. 1970.

FIGS. 29–31, MAP 3

21320 *Cyathea balanocarpa* D. C. Eaton, Mem. Amer. Acad. n. s., 8: 215. 1860. TYPE: Cuba orientali (Oriente), 1859, 1860, *C. Wright 1063*, YU! (two sheets); isotypes: GH!,MO!,NY!,US!.

Stem to 7 m. tall and 14 cm. in diameter, bearing brown scales especially toward the apex and blackish spines to 5 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 5 mm. long and brown scales with a dark apical seta 0.25–0.4 mm. long and without lateral setae. *Petiole* to 0.3 m. long, brown to grayish-brown with blackish spines to 6 mm. long, the scales on the abaxial surface sparingly persistent, nearly uniformly brown with a dark apical seta to 0.25 mm. (occasionally to 0.5 mm.) long and without lateral setae. *Lamina* rigidly papyraceous, to ca. 2.5 m. long and 0.7 m. wide, bipinnate-pinnatilobate to bipinnate-pinnatifid (predominately pinnate-pinnatisect to bipinnate), with a gradually acute apex. *Rachis* brown, adaxially furfuraceous-pubescent, abaxially furfuraceous-glabrescent to furfuraceous-pubescent distally. *Central pinnae* sessile, narrowly triangular to narrowly ovate-lanceolate, to 34 cm. long and 6.5 cm. wide; *basal pinnae* highly reduced to ca. 4 cm. long but not sub-aphlebioid in structure; *pinna-rachis* or *costa* adaxially pubescent with occasionally intermixed long narrow tan scales, abaxially furfuraceous-squamose to pubescent distally, lateral pneumatodes at costule axils lacking or inconspicuous, not alate. *Pinnules* or *pinnule-segments* to ca. 3.3 cm. long and 0.6 cm. wide, straight to sub-falcate with lateral margins entire-undulate to dentate-lobate (the teeth mostly simple) and usually auriculate especially on the basiscopic side, apex entire to serrulate, margins slightly or not revolute, the more or less central pinnules sessile, to partially adnate, basal pinnules often pinnatilobate to pinnatifid and to 1 mm. petiolulate; *costa* or *costule* adaxially sparsely pubescent to glabrescent, abaxially stiffly pubescent and with occasional flat to bullate usually dark-setate squamules to ca. 0.5–1.0 mm. long, not significantly clustered in the axil; *veins* once or more forked,

near to ca. 0.5 mm. from the axis, in strongly lobate pinnule-segments and in the basal auricles the veins borne on a secondary axis, evident on both surfaces, adaxially glabrous, abaxially glabrous or rarely with occasional stiff trichomes on the veins of a secondary axis; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the primary forking of the veins; *indusium* cyathiform, occasionally meniscoid or urceolate, brown, of more or less firm texture and mostly entire at maturity, persistent, glabrous; *receptacle* columnar to globose, inserted to exserted, with sparse paraphyses to 0.2–0.3 mm. long.

The pinnules and pinnule-segments of this species are usually persistent but may infrequently drop off in herbarium material. Although the fertile pinnules in *Nephelea* are often somewhat more contracted than their sterile counterparts, this condition is occasionally more pronounced in *N. balanocarpa*. Such characters are considered to be random, trivial, and are not of taxonomic importance.

Nephelea balanocarpa is endemic to the mountains of Cuba, where it is known only from the provinces of Oriente and Las Villas (formerly Santa Clara). It is found at altitudes of 750–1350 m. (with one collection from about 400 m.) in sink holes and ravines and in wet or dwarf forest on mountain slopes.

ADDITIONAL SPECIMENS EXAMINED: **Cuba. Oriente:** *Clément 751* (F,US), *826, 995, 1272, 1659, 7571* (US), *1652* (UC), *1653* (GH), *1667, 1676* (M); *Ekman 1639, 5326, 8132* (S,US), *3872* (US), *5163, 14645* (S); *Hioram 7002, 7292, 7294, 7296, 7300, 7305, 7309* (US); *Hioram & Clément 1653* (GH), *6372, 6408* (US); *León 11174* (NY,US), *11182* (NY), *14021*(US); *León, Clément & Roca 10116, 10531* (US), *10215* (NY,US); *Maxon 4031* (GH,M,NY,UC,US); *Morton & Acuna 3677* (US); *Shafer 8033, 8224* (US); *Taylor 508* (NY). **Las Villas** (formerly Santa Clara): *Bailey 12453* (US); *Jack 7115, 7132, 7879* (F,GH,NY,US), *7248* (F,GH,MO,NY,US), *8053* (GH,US); *Jack & Rowe 10421* (NY); *Morton 4238* (GH,UC,US).

3. **Nephelea Grevilleana**

(Mart.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

FIGS. 32–35, MAP 4

Cyathea Grevilleana Mart. Icon. Pl. Crypt. Bras. 78. 1834. TYPE: Jamaica, comm. *Greville* in 1832, BR!, fragment US! ex BR, fragment and photo BM! ex BR.

Cyathea elegans Hew. Mag. Nat. Hist. II, **2**: 466. 1838. TYPE: Jamaica, Parish of St. Elizabeth or Manchester, 1823–1826, *Heward*, K (not seen), fragment NY! ex herb. Heward at K; isotypes: BM (fide Rolla Tryon, 1969), P!

Cyathea arborea var. *pallida* Hook. Sp. Fil. 1: 17. 1844. Based on *C. elegans* Hew.

Stem to 6 m. tall and 8.5 cm. in diameter, bearing brown scales especially toward the apex and blackish spines to 9 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 13 mm. long and brown scales with a dark apical seta 0.25 mm. or less long (rarely additional inconspicuous setae toward the scale apex). *Petiole* to 0.05–0.25 m. long to the sub-aphlebioid basal pinnae, brown to grayish-brown with blackish spines to 6 mm. long, the scales on the abaxial surface sparingly persistent, dark brown with slightly lighter margins, with a dark apical seta to 0.1–0.25 mm. long and without lateral setae. *Lamina* papyraceous, occasionally rigidly so, to 3.3 m. long and ca. 1.3 m. wide, tripinnate (predominantly bipinnate-pinnatifid), with a gradually acute apex. *Rachis* light brown, adaxially minutely furfuraceous to pubescent, abaxially glabrous. *Central pinnae* sessile to short (to ca. 0.5–1.0 cm.) petiolulate, ovate-lanceolate, to ca. 70 cm. long and 20 cm. wide; *basal pinnae* highly reduced, often to 8 cm. or less long and usually sub-aphlebioid in structure; *pinna-rachis* adaxially pubescent (very rarely with occasional long narrow tan scales),

abaxially furfuraceous-glabrescent to pubescent distally, with usually conspicuous lateral pneumatodes at costa axils, often narrowly greenish-alate (to ca. 0.25 mm. wide on each side) between the most distal sessile pinnules. *Pinnules* to 12 cm. long and 3 cm. wide, deeply pinnatifid (pinnate at the base), sessile, ovate or elliptic to obovate, the apex more or less acute; *costa* adaxially pubescent, abaxially squamose to furfuraceous-glabrescent and pubescent distally, the distal scales bullate and apically dark-setate, not significantly clustered in the axil. *Segments* subfalcate to falcate with lateral margins serrate-dentate (the teeth usually shallowly bifid, corresponding to the vein endings), apex serrate, margins slightly or not revolute; *costule* adaxially usually with one to few stiff trichomes distally, abaxially pubescent and with usually dark-setate bullate scales; *veins* once-forked at or near the costule to occasionally twice or three times forked, evident on both surfaces, adaxially and abaxially glabrous; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the primary forking of the veins; *indusium* cyathiform to urceolate, brown, of firm texture, persistent and usually entire at maturity, glabrous or occasionally with infrequent small (ca. 0.2–0.3 mm. long) bullate squamules; *receptacle* columnar to globose, mostly inserted, with inconspicuous, short (ca. 0.2–0.3 mm. long), rarely squamuloid, paraphyses.

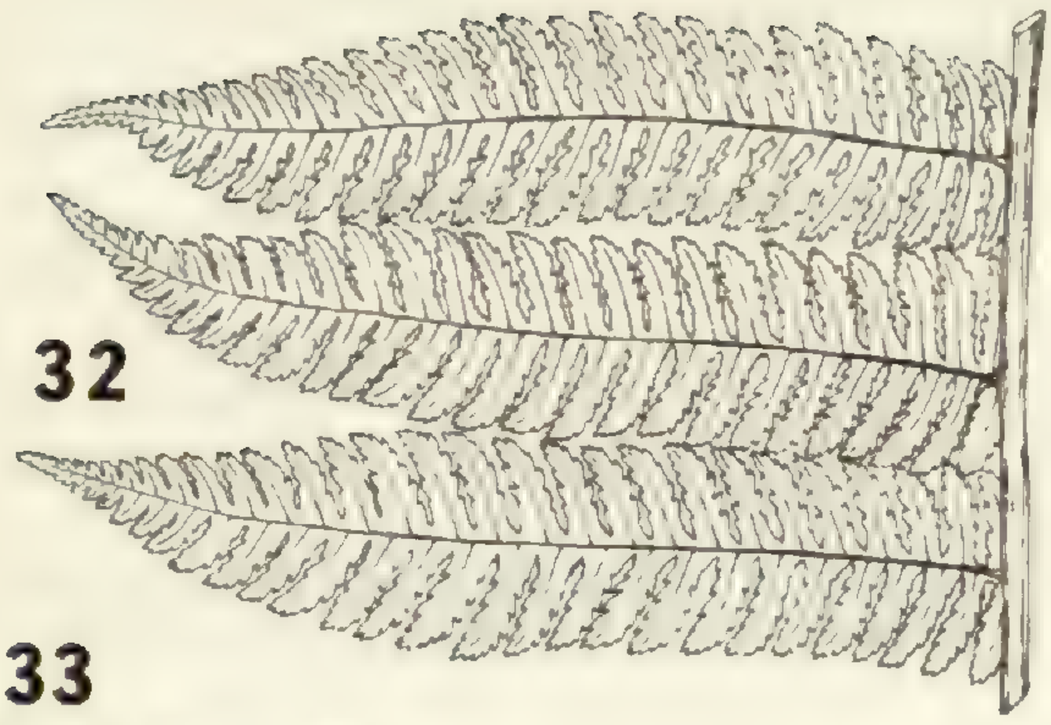
Three sheets in the Jenman herbarium at NY! bear an apparently unpublished varietal epithet referring to the coriaceous texture of the specimens; these specimens are within the normal range of variation of the species.

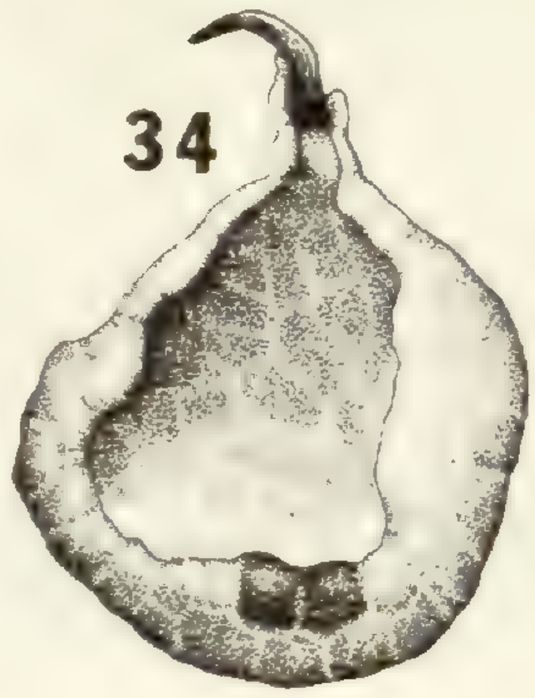
A noteworthy character of this species is the presence of sub-aphlebioid pinnae toward the base of the lamina. Such sub-skeletonized pinnae are uncommon in *Nephelea*, being found elsewhere only in *N. pubescens* and *N. setosa* (Fig. 61). However, these sub-aphlebioid basal pinnae are not always present in *N. Grevilleana*. They are clearly present in fourteen of the eighteen collections I have studied which include the petiole base. Recently in Jamaica I examined and collected three individuals clearly of this species, two of which *(Gastony & Gastony 967, 976)* lacked any indication of these structures.

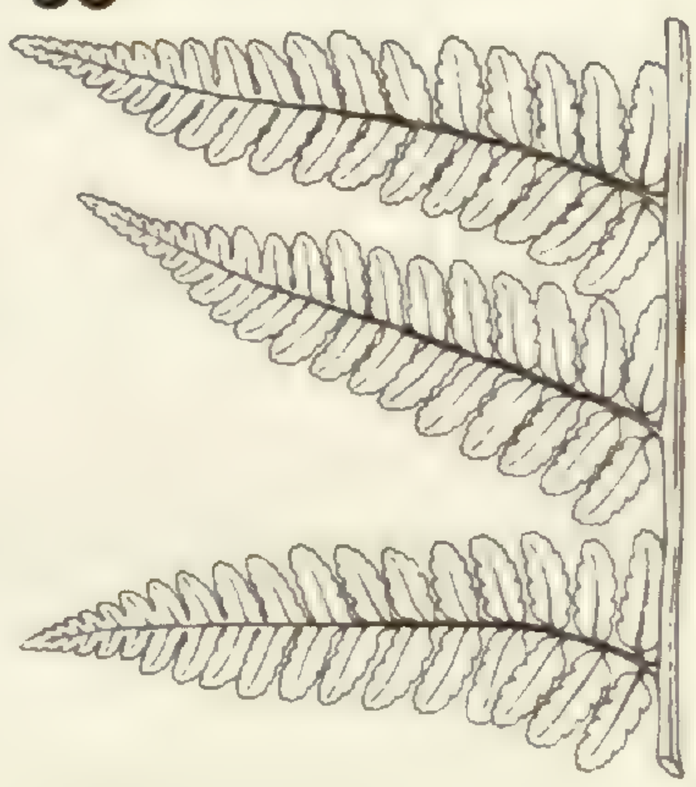
Another interesting feature of *Nephelea Grevilleana* is the occasional squamuloid nature of the paraphyses at the apex of the receptacle. These are uncommon in other species of *Nephelea*, but appear to be more frequent here. Morphologically, they seem to be derived from abortive sporangia and their apical position on a receptacle which develops its sporangia somewhat acropetally suggests they may be related to nutritional or other metabolic inadequacies. These structures are best observed in immature sori, where they comprise a sort of cushion within the opening of the more or less urceolate indusium. Their possible role in protecting the immature sporangia from desiccation or other environmental hazards at the mouth of the indusium possibly confers a selective advantage to plants possessing them.

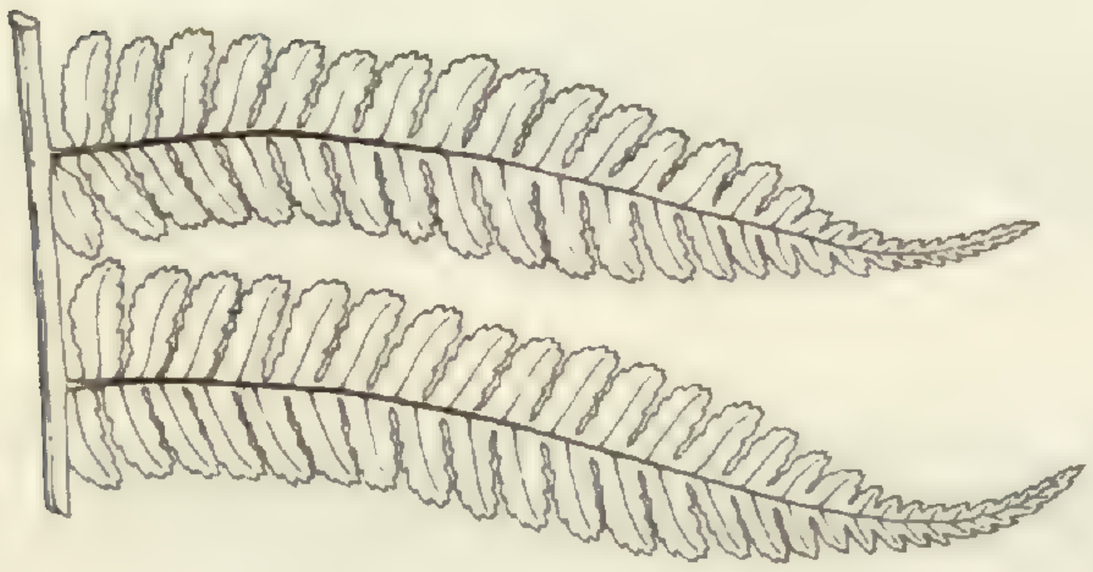
This species is endemic to Jamaica, where it occurs widely at altitudes of 200–950 m. in moist ravines and river valleys or in dense, wet forests, especially on cloud bathed mountain slopes. It is reported to be found on limestone and metamorphic rock.

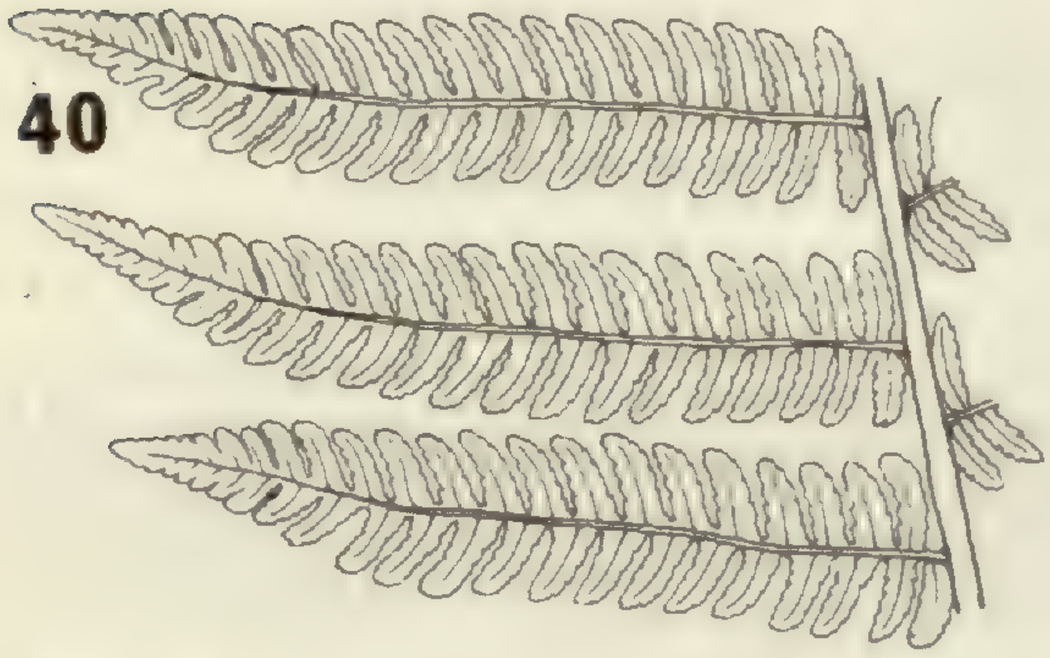
ADDITIONAL SPECIMENS EXAMINED: **Jamaica. Portland:** *Clute* (NY); *Gastony & Gastony 967, 971* (GH); *Maxon 9341* (GH,US); *Maxon & Killip 149, 820* (F,GH,NY,US).











FIGS. 32–35. Nephelea Grevilleana: 32, Central pinnules of a central pinna, *Proctor 4815* (MO), × 0.5; 33, Central portion of a pinnule in 32, × 2; 34, 35, Two views of dark-setate, pouch-like bullate scales from the adaxial costule surface, both *Gastony 101* (GH), × 85. FIGS. 36, 37. Nephelea crassa: 36, Central pinnules of a central pinna, *Ekman H15294* (S), × 0.5; 37, Central portion of a pinnule as shown in 36, *Ekman H15723* (F), × 1.5. FIGS. 38, 39. Nephelea fulgens: 38, Central pinnules of a central pinna, *Gastony et al. 603* (GH), × 0.5; 39, Central portion of a pinnule in 38, × 2. FIGS. 40, 41. Nephelea portoricensis: 40, Central pinnules of a central pinna, *Sintenis 2594* (GH), × 0.5; 41, Central portion of a pinnule as shown in 40, *Britton et al. 3909* (F), × 1.5.

St. Thomas: *Day 2, 3, 4* (NY); *Fredholm 3236* (US); *Gastony 101* (GH); *Hatch 14* (NY,UC,US); *Maxon 2403, 2443* (NY,US) *8896, 9165* (GH,NY,US); *Proctor 3962* (MO,US); *Wilson & Murray 561* (A,US). **St. Thomas-St. Andrew:** *Maxon 10321* (GH,NY,US). **St. Andrew:** *Fisher 65* (NY); *Gastony 27* (GH); *Maxon 1020* (US); *Maxon & Killip 1358* (F,GH,NY,US); *Proctor 4815* (MO); *Underwoood 1584, 1585, 1624* (NY). **St. Catherine-St. Ann:** *Day 130* (GH,NY); *Maxon 1945, 10453* (US); *Underwood 1820* (NY). **St. Ann:** *R. C. Alexander* (US); *Campbell or Harris 7725* (F,NY,US); *Hatch 10* (US); *Howard & Proctor 15163* (A); *Jenman* (NY); *Orcutt 6078* (F,GH,MO,NY,UC); *Proctor 15515* (A). **Manchester:** *Jenman* (NY). **Trelawny:** *Gastony & Gastony 976* (GH). **St. Elizabeth:** *Maxon & Killip 1473* (F,GH,NY,US). **Westmoreland:** *Proctor 4633* (US); *Wilson & Webster 505* (A,US).

4. **Nephelea crassa** (Maxon) Tryon, Contrib. Gray Herb. 200: 38. 1970.

Figs. 36, 37, Map 5

Cyathea crassa Maxon, Contrib. U.S. Nat. Herb. 13: 40. 1909. TYPE: Santo Domingo (Dominican Republic) in sylva montis "Isabel de la Torre," 550 m., 8 VII 1887, *Eggers 2735c*, US 523878! (incorrectly cited by Maxon as *523876*); isotype: US!.

Cyathea domingensis Brause, in Urban, Symb. Ant. 7: 153. 1911. TYPE: Santo Domingo (Dominican Republic) ad Maniel prope Barahona 600 m. alt. in sylvis montanis, Dec. 1908, *H. von Türckheim 2715*, presumably at B (not seen); isotypes: F!,GH!,MO!,NY!,P!,US!.

Stem to 7.5 m. tall and 7 cm. in diameter, bearing brown scales especially toward the apex and blackish spines to 5 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 5 mm. long and brown scales with a dark apical seta 0.25 mm. or less long. *Petiole* to ca. 0.13–0.38 m. long, brown to purple-brown with blackish spines to 9 mm. (usually less) long, the scales on the abaxial surface sparingly persistent, brown, with a dark apical seta to 0.5 mm. (usually less) long and without lateral setae. *Lamina* rigidly papyraceous, to ca. 1.7 m. long and 1.2 m. wide, tripinnate (predominantly bipinnate-pinnatifid), with a more or less gradually acute apex. *Rachis* brown, adaxially minutely pubescent to glabrescent, abaxially glabrous. *Central pinnae* sessile to short (to ca. 1 cm.) petiolulate, ovate-lanceolate, to 60 cm. long and 21 cm. wide; *basal pinnae* highly reduced, to ca. 8 cm. long; *pinna-rachis* adaxially pubescent, abaxially furfuraceous to mostly glabrescent, with mostly inconspicuous lateral pneumatodes at costa axils, usually narrowly greenish–alate (to ca. 0.25 mm. wide on each side) between the most distal sessile pinnules. *Pinnules* to ca. 11 cm. long and 3 cm. wide, deeply pinnatifid (pinnate at the base), sessile to short (to 1.5 mm.) petiolulate, narrowly triangular to narrowly ovate, the apex acuminate; *costa* adaxially more or less sparsely pubescent to glabrescent distally, abaxially sparsely and minutely squamose to glabrescent, often not pubescent distally, the scales not significantly clustered in the axil. *Segments* straight to sub-falcate with lateral margins serrate-crenate (the teeth often shallowly to moderately bifid, corresponding to the vein endings), or rarely pinnatilobate to pinnatifid, apex serrate-crenate, margins slightly or not revolute; *costule* adaxially glabrous, abaxially glabrescent or sparsely pubescent and squamose with dark-setate bullate scales; *veins* once-forked near to 0.5 mm. from the costule, more forked in more highly toothed or lobed segments, evident on both surfaces, adaxially and abaxially glabrous; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the primary forking of the veins; *indusium* cyathiform to urceolate, brown, of firm texture, persistent and usually entire at maturity, glabrous; *receptacle* columnar, inserted to slightly exserted, with sparse short (ca. 0.2–0.4 mm. long) paraphyses.

Although the more strongly squamuloid paraphyses occasionally found in *Nephelea Grevilleana* have not been observed in this species, the morphology of some of the larger paraphyses here is also suggestive of

sporangial derivation. This is especially true of paraphyses found toward the apex of the receptacle.

Nephelea crassa appears to be closely related to *N. Grevilleana* and there has been some confusion between them in the past. Specimens from the Barahona province of the Dominican Republic in particular caused Maxon (1924, 1937 in Christensen) to vacillate in his recognition of these two taxa. He finally concluded that some Barahona specimens were *Cyathea elegans*. These specimens have also proved difficult for me, but I now feel confident that they are *N. crassa* and that *N. Grevilleana* does not occur in Hispaniola. These specimens are similar to *N. Grevilleana* in their cutting and the squamose indument on the abaxial costule surface, but I have seen no material of *N. crassa* with sub-aphlebioid basal pinnae, even though these pinnae may be quite reduced in size. Furthermore, the specimens most like *N. Gravilleana* in their cutting lack the stiff trichomes on the adaxial costule surface which characterize that species.

Most specimens of *Nephelea crassa* have a glabrous or glabrescent abaxial costule surface. Maxon took this to represent the total variation of the species, but the more extensive collections now available for study show that this represents only one extreme of the total species variation. There is a clinal variation indicated by a higher incidence of scales and pubescence on the abaxial costule surface in the western and southwestern (Barahona) part of the species range to glabrescence in the northeast and east. This supports the view that the species originated in the western and southwestern portions of Hispaniola from an ancestor common to it and *N. Grevilleana*, that it lost the more primitive sub-aphlebioid condition of the basal pinnae, and that as it migrated to the east and northeast most of the costule indument was lost, while the pinnules became more triangular with a more prolonged apex.

This species is endemic to Hispaniola where its range extends nearly throughout the length of the island mostly at altitudes of 100–600 m., although it also has been collected at 1065 m. and 1250 m. It is found in moist ravines and lowland rain forest and occasionally on mountain slopes.

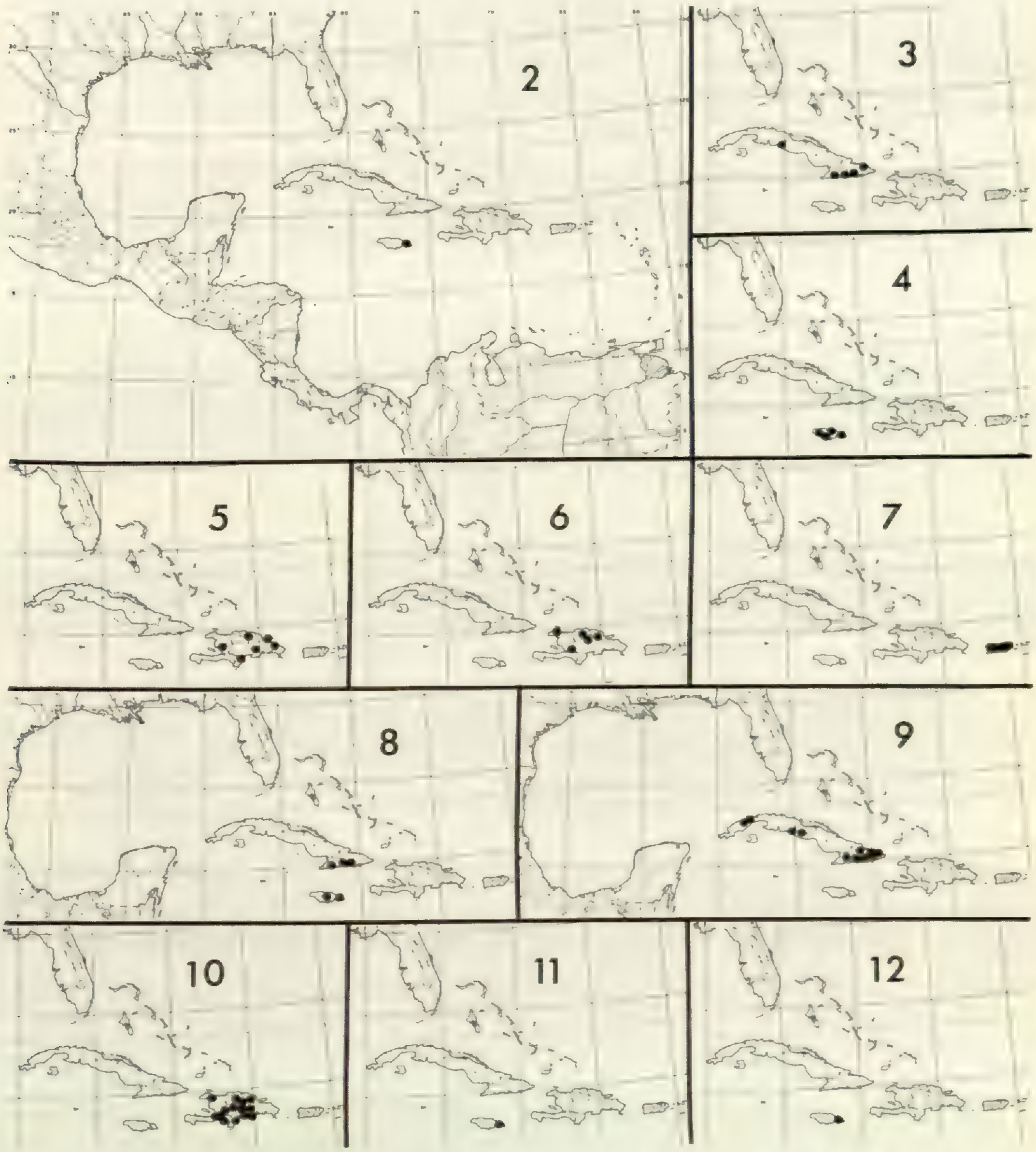
ADDITIONAL SPECIMENS EXAMINED: **Dominican Republic. El Seibo:** *Abbott 2662* (GH,US); *Ekman H15723* (F,S); *Gastony et al. 647* (GH,NY,US). **Samaná:** *Ekman H15119* (GH,US), *H15294* (NY,S,US). **San Cristobal** (formerly Santo Domingo): *Ekman H11500* (F,NY). **Puerto Plata:** *Eggers 2735* (F,US); *Ekman H14430* (NY,S,US). **Barahona:** *Fuertes 741* (NY,US), *742* (F,GH,MO); *Howard 8483* (GH,NY,US); *Türckheim 2714* (F,GH,MO,NY), *2716* (US). **Haiti. Ouest:** *Ekman H5522* (US).

5. **Nephelea fulgens** (C. Chr.) Gastony, comb. nov.

FIGS. 38, 39, MAP 6

Cyathea fulgens C. Chr. Kungl. Svensk. Vetens.-akad. Hand. ser. 3, **16**: 14. t. 1 (Figs. 9–12). 1937. TYPE: Haiti, Nord, St. Louis du Nord, Morne Chavary, 900 m., on laterite, 25 Aug. 1925, *Ekman H4721* s!; isotype: us! (two sheets).

Stem to 4 m. tall and 6.5 cm. in diameter, bearing brown scales especially toward the apex and blackish spines to 9 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 7 mm. long and brown scales with a dark apical seta ca. 0.25 mm. long and without lateral setae. *Petiole* to 0.36 m. long, dark brown, with blackish spines to ca. 10 mm. long, the scales on the abaxial surface usually deciduous above their blackish spine-like bases, leaving a scabrous surface, brown with a blackish central stripe, with a dark apical seta to 0.1–0.2 mm. long and without lateral setae. *Lamina* coriaceous to ca. 2 m. long and 1.2 m. wide, tripinnate to tripinnate-pinnatifid (predominately bipinnate-pinnatifid), with a gradually acute apex. *Rachis* dark brown, adaxially minutely pubescent to glabrescent, abaxially glabrescent to glabrous. *Central pinnae* sessile to short (to ca. 1.5 cm.) petiolulate, ovate-lanceolate, to ca. 55 cm. long and 16 cm. wide; *basal pinnae* reduced, often to ca. 10 cm. long; *pinna-rachis* adaxially pubescent, abaxially furfuraceous to mostly glabrescent, with usually inconspicuous lateral pneumatodes at costa axils, not conspicuously greenish-alate between the most distal sessile pinnules. *Pinnules* to ca. 9 cm. long and 2.5 cm. wide, deeply pinnatifid, (pinnate to pinnate-pinnatifid at the base), short (to ca.



MAPS 2–12. 2, Nephelea pubescens; 3, N. balanocarpa; 4, N. Grevilleana; 5, N. crassa; 6, N. fulgens; 7, N. portoricensis; 8, N. woodwardioides var. woodwardioides; 9, N. woodwardioides var. cubensis; 10, N. woodwardioides var. Hieronymi; 11, N. Tussacii; 12, N. concinna.

2 mm.) petiolulate, triangular, the apex more or less acute; *costa* adaxially sparsely pubescent to glabrescent, abaxially sparsely squamose to glabrescent, usually sparsely pubescent distally, the scales not significantly clustered in the axil. *Segments* straight to sub-falcate, with lateral margins subentire to crenate (basal segments of some pinnules pinnatilobate to pinnatifid), the apex subentire to crenulate, margins not revolute; *costule* adaxially glabrous, abaxially sparsely pubescent and with sparse bullate to sub-bullate scales to ca. 0.5–1.0 mm. long and usually with one or more dark apical setae; *veins* mostly once-forked at or near the costule, more forked or borne on secondary costules in more strongly crenate to lobed segments, evident on both surfaces, adaxially and abaxially glabrous; *lamina surface* adaxially and abaxially glabrous between the veins, at 15× magnification the dried adaxial surface usually appearing reticulate and the stomata visible abaxially. *Sori* at the primary forking of the veins; *indusium* sphaeropteroid to sub-sphaeropteroid, brown, of more or less firm texture, persistent but rupturing into usually 2–3 lobes at maturity, glabrous; *receptacle* globose to columnar, inserted, paraphyses to 0.1–0.4 mm. long.

As in the case of *Nephelea crassa*, the morphology of the larger paraphyses of *N. fulgens* suggests their sporangial derivation. Unlike all other Greater Antillean species of *Nephelea*, which have meniscoid to cyathiform or urceolate indusia, the indusia of *N. fulgens* are sphaeropteroid to sub-sphaeropteroid. It is further distinguished from *N. crassa*, which may be its closest relative, by its coriaceous to strongly coriaceous lamina texture, the more blunted teeth of its ultimate segments, the usually conspicuous (at a magnification of 15× or more) stomatal apparatus abaxially and reticulate pattern of the dried lamina surface adaxially, the greater scabrosity of the petiole base due to the persistent bases of the more indurated scales, and by its occurrence at generally higher altitudes.

Nephelea fulgens is endemic to Hispaniola, where it occurs at altitudes of ca. 800–2000 m. on shrubby to forested moist mountain slopes. It is reported from lateritic and calcareous soils.

ADDITIONAL SPECIMENS EXAMINED: **Dominican Republic. Duarte** (formerly part of Pacificador): *Abbott 2068* (GH,NY,US); *Ekman H12279* (S,US). **Santiago:** *Jiménez 3863* (US). **Santiago Rodriguez** (formerly part of Monte Cristi): *Ekman H12862* (S,US). **San Rafael:** *Gastony et al. 506, 603* (GH,NY,US).

6. Nephelea portoricensis

(Kuhn) Tryon, Contrib. Gray Herb. 200: 40. 1970.

FIGS. 40, 41, MAP 7

Cyathea portoricensis Spreng. ex Kuhn, Linnaea 36: 163. 1869. TYPE: Puerto Rico, *Balbis*, perhaps B (not seen); isotypes: B! in herb. Kunth, NY! fragment of isotype or possibly of holotype ex herb. B, possible isotype portion P! herb. Luerssen 10486 ex herb. LZ.

Stem to 4 m. tall and 6.5 cm. in diameter, bearing brown scales especially toward the apex and blackish spines to 9 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 11 mm. long and brown scales with a dark apical seta 0.25 mm. or less long and without lateral setae. *Petiole* to ca. 0.5 m. long, dark brown to purple-brown with blackish spines to 8 mm. long, the scales on the abaxial surface brown, often with a darker central stripe, with a dark apical seta to ca. 0.25 mm. long and without lateral setae. *Lamina* rigidly papyraceous, length not known, to ca. 1.2 m. wide, with a gradually acute apex. *Rachis* dark brown to purple-brown, adaxially pubescent and occasionally squamose, abaxially glabrescent. *Central pinnae* sessile to

short (to ca. 1 cm.) petiolulate, ovate-lanceolate, to 66 cm. long and 23 cm. wide; *basal pinnae* not highly reduced, to ca. 20 cm. or more long; *pinna-rachis* adaxially pubescent, often with occasional long, narrow, tan to brown scales, abaxially furfuraceous to mostly glabrescent, pubescent distally, lateral pneumatodes at costa axils not evident, not greenish-alate between the most distal sessile pinnules. *Pinnules* to 9.5 cm. long and 2.5 cm. wide, deeply pinnatifid (pinnate to pinnate-pinnatilobate at the base), sessile, ovate, the apex bluntly acute; *costa* adaxially pubescent, abaxially stiffly pubescent (especially distally) and more or less brown squamose, the scales with one to several dark apical setae, not significantly clustered in the axil. *Segments* sub-falcate with lateral margins subentire to crenate-serrate, apex crenulate-serrulate, margins slightly or not revolute; *costule* adaxially glabrous or with one to few stiff trichomes distally, abaxially pubescent and with flat to sub-bullate squamules (to ca. 0.25 mm. long) with several dark apical and lateral setae; *veins* once forked or occasionally more branched at, or about 0.5–1.0 mm. from, the costule, evident on both surfaces, adaxially glabrous, abaxially usually with stiff trichomes; *lamina surface* adaxially and abaxially glabrous (rarely abaxially pubescent) between the veins. *Sori* at the primary forking of the veins; *indusium* cyathiform to urceolate, brown (at maturity), of firm texture, persistent, and usually entire at maturity, pubescent with more or less stiff white trichomes (rarely these trichomes bi-seriate to multi-seriate and squamuloid, or with actual squamules); *receptacle* globose to occasionally columnar, inserted, with inconspicuous paraphyses 0.1–0.2 mm. long.

Nephelea portoricensis is the only species of *Nephelea* in the West Indies with pubescent indusia. Its affinities are certainly with the other Greater Antillean *Nephelea* species, although unlike them the scales on its abaxial costae and costules are never more than sub-bullate.

A collection from Indiera Fria, near Maricao *(Britton, Cowell & Brown 4520)*, is peculiar in its very narrow pinnae (largest pinnules ca. 4 cm. long and 1 cm. wide). However, the critical characters of the material are certainly those of *Nephelea portoricensis*. Evidently a juvenile form is represented.

Nephelea portoricensis is endemic to Puerto Rico and is the only species of *Nephelea* on the island. It occurs at altitudes of ca. 500–1100 m. in ravines and on forested mountain slopes in a more or less central band nearly throughout the length of the island.

ADDITIONAL SPECIMENS EXAMINED: **Puerto Rico.** *Blomquist 11733* (UC), *11965* (F), *13134* (US); *Britton & Britton 7207* (NY,US); *Britton & Cowell 913* (NY,US); *Britton et al. 3909, 6550, 6865* (F,NY,US), *4520, 8378* (NY,US), *5593* (F,MO,NY,US); *Cowgill 619* (US); 1921, *English* (US); *Hioram 255, 260* (US); 1924, *Kern & Whetzel* (US); *Sargent 333* (US); *Scamman 6518* (GH); *Shafer 3499* (F,MO,NY,US); *Sintenis 2594* (GH,M,NY,US), *2654* (F,MO,NY), *4102* (A,GH,US), *6158* (GH,M,US); *Stevens 1411* (NY); *Tryon & Tryon 7082, 7085* (GH); *Underwood & Griggs 272* (NY).

21245 **7. Nephelea woodwardioides** (Kaulf.) Gastony, comb. nov.

21239 *Cyathea woodwardioides* Kaulf. Enum. Fil. 255. 1824. TYPE: without collector or locality, presumably destroyed at LZ; fragment "Ex Herb. Kaulf. fragm. origin., ohne standortsangabe" P!.

Stem to 9 m. tall and 30 cm. in diameter (including the investing sheath of adventitious roots), bearing brown scales especially toward the apex and blackish spines to 15 mm. long, occasionally with adventitious buds. *Unexpanded croziers* with blackish spines to 8–15 mm. long and brown scales with a dark apical seta to 0.25–0.5 mm. long and without lateral setae. *Petiole* to ca. 0.5 m. long, stramineous to dark

brown with blackish spines to 8–14 mm. long, the scales on the abaxial surface sparingly persistent, brown with a dark apical seta to 0.25 mm. long and without lateral setae. *Lamina* rigidly papyraceous to coriaceous, to ca. 2.5 m. long and 1.3 m. wide, tripinnate (predominately bipinnate-pinnatifid), with the apex more or less gradually acute or occasionally more abruptly reduced and pinna-like. *Rachis* stramineous to brown or purple-brown, adaxially and abaxially furfuraceous-glabrescent. *Central pinnae* sessile to short (to ca. 1–2.5 cm.) petiolulate, ovate-lanceolate to narrowly so, to ca. 64 cm. long and 18–23 cm. wide; *basal pinnae* quite reduced, to ca. 18–25 cm. long; *pinna-rachis* adaxially pubescent, occasionally with scattered long, narrow, tan to brown scales, abaxially furfuraceous to glabrescent (with occasional blackish-centered scales in some), pubescent distally, with mostly inconspicuous to swollen, dark, conspicuous lateral pneumatodes at costa axils, not greenish-alate between the most distal sessile pinnules. *Pinnules* to ca. 10 cm. long and 2.2 cm. wide, deeply pinnatifid (pinnate at the base), sessile to short (to ca. 1.5–3 mm.) petiolulate narrowly ovate to triangular or elliptic, the apex acute to acuminate; *costa* adaxially pubescent, some with occasional long, narrow, brown scales proximally and glabrescent distally, abaxially furfuraceous-squamose to glabrescent, more or less pubescent distally, the scales to ca. 1–1.5 mm. long with brown to black centers and lighter margins and with one to several dark apical setae, not significantly clustered in the axil. *Segments* straight to sub-falcate or falcate with lateral margins entire to serrate-crenate (rarely especially the basal segments lobate), apex subentire to serrate-crenate, margins slightly revolute; *costule* adaxially glabrous or rarely with one to several stiff trichomes distally, abaxially with apically dark-setate bullate to sub-bullate scales to 0.5–1.0 mm. long and pubescent to glabrescent distally; *veins* once-forked at or near the costule, occasionally more forked, evident on both surfaces or somewhat obscure adaxially, adaxially and abaxially glabrous; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the primary forking of the veins; *indusium* cyathiform to urceolate, brown, of more or less firm texture, persistent and entire at maturity, glabrous; *receptacle* globose to columnar, inserted to exserted, with mostly inconspicuous short (to 0.2 mm. long) paraphyses.

KEY TO VARIETIES

Axes usually dark; axil of costa (and occasionally of costules) with a conspicuously prominent dark pneumatode; lamina coriaceous; (segment margins entire to subentire, very rarely serrate-crenate; costule abaxially stiffly pubescent, occasionally sparsely so, and with bullate to sub-bullate scales; centers of largest scales on abaxial costa surface brown to blackish-brown). Jamaica, Cuba .. 7a. var. *woodwardioides*.

Axes usually stramineous to light brown; axil of costa without a dark pneumatode or the pneumatode not conspicuously prominent; lamina rigidly papyraceous to subcoriaceous.

Segment margins subentire to (especially at the apex) serrate-crenate; costule abaxially sparsely pubescent to glabrescent distally and with bullate to sub-bullate scales; centers of largest scales on abaxial costa surface mostly brown (occasionally blackish-brown). Cuba. ..... 7b. var. *cubensis*.

Segment margins entire to serrate-crenate; occasionally costule abaxially pubescent distally and with bullate to sub-bullate scales; centers of largest scales on abaxial costa surface blackish-brown to black. Hispaniola ..... 7c. var. *Hieronymi*.

7a. **Nephelea woodwardioides** var. **woodwardioides**

FIGS. 42–44, MAP 8

Cyathea nigrescens Auct. not (Hook.) J. Sm., e.g. Maxon North Amer. Fl. 16: 74. 1909.

Cyathea araneosa Maxon, North Amer. Fl. 16: 74. 1909. TYPE: Cuba, Oriente, upper slopes and summit of Gran Piedra, 900–1200 m., April 14, 1907, *Maxon 4035, US 522680!*; isotypes: F!,GH!,M!,NY!,UC!,US!.

Nephelea araneosa (Maxon) Tryon, Contrib. Gray Herb. 200: 38. 1970.

Cyathea hystricosa Mort. Amer. Fern Jour. **55**: 30. 1965. TYPE: Jamaica, ca. 1805 *Wiles*, BM, Morton photo 8097 (not seen; from the description and cited specimens there is no doubt as to the identity).

Adventitious buds on the stem not known. *Unexpanded croziers* with blackish spines to 10 mm. long and brown scales with a dark apical seta 0.25 mm. or less long. *Petiole* to 0.45 m. long, dark brown, with blackish spines to 11 mm. long, the scales on the abaxial surface sparse or deciduous. *Lamina* coriaceous, with a more or less gradually acute apex. *Rachis* brown to purple-brown. *Central pinnae* sessile to short (to ca. 1 cm.) petiolulate, ovate-lanceolate, to 63 cm. long and 18 cm. wide; *basal pinnae* quite reduced to ca. 19 cm. long; *pinna-rachis* abaxially furfuraceous-glabrescent, pubescent distally, with swollen, dark, conspicuous lateral pneumatodes at costa axils. *Pinnules* sessile to short (to ca. 3 mm.) petiolulate, narrowly ovate to triangular; *costa* adaxially pubescent with occasional long, narrow, brown scales proximally and glabrescent distally, abaxially furfuraceous-squamose to glabrescent, pubescent distally, the scales with more or less dark brown centers. *Segments* falcate to sub-falcate with lateral margins entire to subentire (rarely serrate-crenate above the basal segments), apex subentire to serrate-crenate; *costule* adaxially glabrous, abaxially stiffly pubescent (occasionally sparsely so) and with apically dark-setate bullate to sub-bullate scales.

This variety is best distinguished by the usually quite conspicuous pneumatodes at the costa axils and occasionally at the costule axils. Similar but much less conspicuously developed pneumatodes are frequently found in other species of *Nephelea* at the costa axils, but only in this variety have they been observed (occasionally) at the costule axils.

The portion of the holotype of *Cyathea woodwardioides* Kaulf. that I have seen is only a fragment; however, the application of the name is certain from its characters. The collection was probably made in Jamaica, where early collectors were active, and where var. *woodwardioides* is common.

In describing *Cyathea araneosa* as new, Maxon was undoubtedly strongly influenced by what appears to be a delicately whitish araneose-ciliate margin of the indusium in the type collection. This condition has also been found in a collection from Jamaica, but in both cases close examination reveals that it is simply a fungus—the mycelium of a species of *Nectria*.

Variety *woodwardioides* occurs in Jamaica at ca. 725–1430 m., predominantly in the Blue and John Crow mountains, with a disjunct station in the mountains of Clarendon. It is found in cloud forest (often associated with *Podocarpus*) and rain forest in exposed and wooded situations on ridges, in ravines, and on mountain slopes. In Cuba it is known in similar habitats only from the most southerly mountains of Oriente (the Sierra Maestra and Gran Piedra) at 900–1200 m. altitude.

ADDITIONAL SPECIMENS EXAMINED: **Jamaica.** *Jenman 41* (UC). **Portland:** *Gastony 93* (GH); *Maxon & Killip 827* (F,GH,NY,US); *Tryon & Tryon 6979* (GH). **St. Thomas:** *Maxon 9219, 9460, 9512, 9557* (NY,US), *9426* (GH,NY,US), *9492* (US). **Portland-St. Andrew:** *Maxon & Killip 984* (F,GH,NY,US). **St. Andrew:** *Johnson 1804* (US); *Proctor 8330* (MO); *Underwood 1549* (NY), *3253* (NY,US); *Von der Porten & Lewis P–336* (US); *Wilson 527* (A,US); *Wilson & Webster 474* (A,US). **Clarendon:** *Underwood 3388* (NY). **Cuba. Oriente:** *Clément 460* (NY,US). *1665* (US); *Hioram 7312* (US); *Hioram & Clément 6374* (US), *6375* (GH,US); *León et al. 10532, 10534* (NY,US).

7b. **Nephelea woodwardioides** var. **cubensis** (Maxon) Gastony, comb. et stat. nov.

FIGS. 45–47, MAP 9

Cyathea cubensis Underw. ex Maxon, North Amer. Fl. **16**: 73. 1909. TYPE: Cuba, Baracoa, base of El Yunque Mt., March 1903, *Underwood & Earle 1313*, NY! (three sheets).

Nephelea cubensis (Maxon) Tryon, Contrib. Gray Herb. 200: 40. 1970.

Adventitious buds on the stem not known. *Unexpanded croziers* with blackish spines to 8 mm. long and brown scales with a dark apical seta to 0.25–0.5 mm. long. *Petiole* to ca. 0.4 m. long, stramineous to light brown, with blackish spines to 8 mm. long, the scales on the abaxial surface usually sparse to few. *Lamina* rigidly papyraceous to sub-coriaceous, with a more or less gradually acute apex. *Rachis* stramineous to brown. *Central pinnae* sessile to short (to ca. 2.5 cm.) petiolulate, ovate-lanceolate, to 64 cm. long and 23 cm. wide; *basal pinnae* quite reduced, to ca. 18 cm. long; *pinna-rachis* abaxially furfuraceous-glabrescent, more or less pubescent distally, with mostly inconspicuous lateral pneumatodes at costa axils. *Pinnules* sessile to short (to ca. 2 mm.) petiolulate, narrowly ovate to elliptic; *costa* adaxially pubescent, glabrescent distally, abaxially furfuraceous-squamose to glabrescent, sparsely pubescent distally, the scales with mostly brown centers. *Segments* straight to subfalcate (rarely falcate) with lateral margins subentire to serrate-crenate (rarely especially the basal segments lobate), apex more strongly serrate-crenate; *costule* adaxially glabrous, abaxially sparsely pubescent to glabrescent distally and with apically dark-setate bullate to sub-bullate scales, these often also with light-colored trichomoid processes.

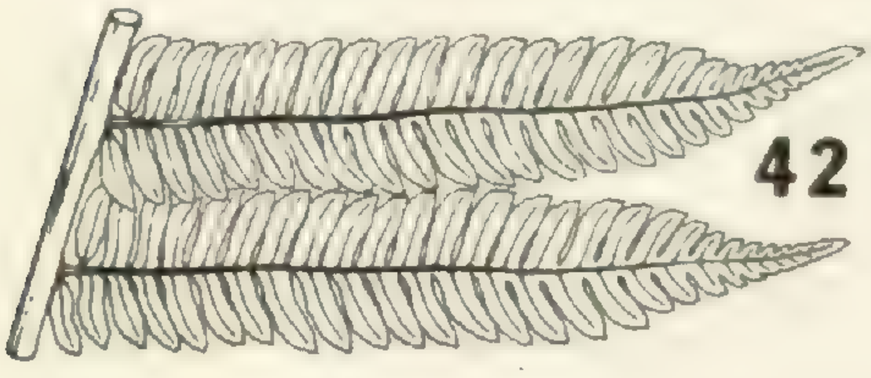
In addition to the characters mentioned in the key, the often abruptly reduced pinna apex (sometimes nearly to the form of a pinnule) helps to distingush this variety. In comparison to var. *Hieronymi*, the ultimate segments in var. *cubensis* are more strongly and more frequently serrate-crenate at the apex. Of the three varieties, var. *cubensis* shows the strongest tendency to possess sub-bullate squamules abaxially on the costule.

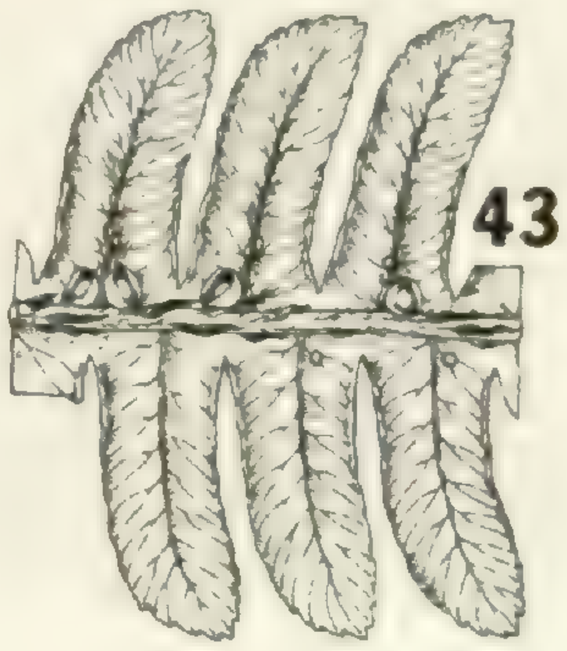
Five collections from the Sierra Maestra *(Ekman 5388, León 11089, Morton 9292* and *9435, Taylor 449)* seem at first rather distinct from var. *cubensis*. Less extreme states of each of the several characters which lend a distinctive appearance to these specimens can be found in other collections of var. *cubensis*. It therefore seems best to regard the material available as representing more or less extreme forms of var. *cubensis*. Perhaps most troublesome are the presence of squamules on the abaxial costule surface which are at most sub-bullate, making these specimens difficult to accommodate in the key to species.

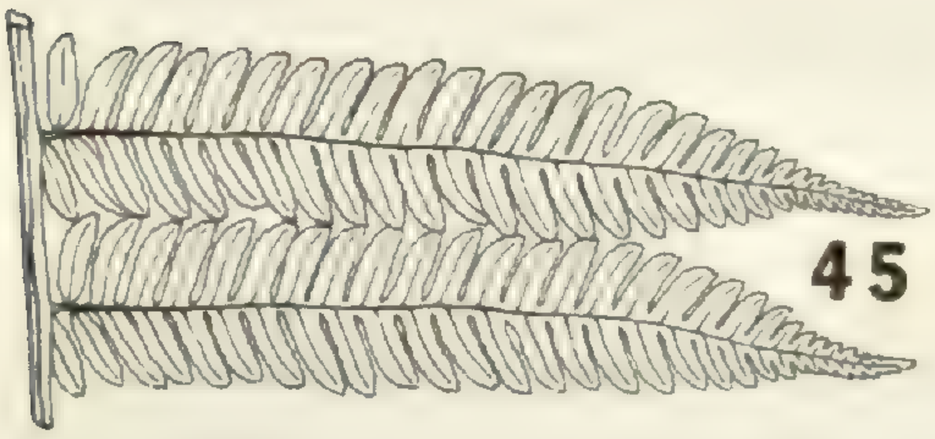
Variety *cubensis* is endemic to Cuba in the three major mountainous areas: southern Oriente, the Sierra de Trinidad in Las Villas, and the Sierra de los Organos in Pinar del Río. It is found in moist situations in ravines and on ridges and mountain slopes in or at the edges of forest at ca. 400–1100 m. altitude, some specimens have been recorded from limestone areas.

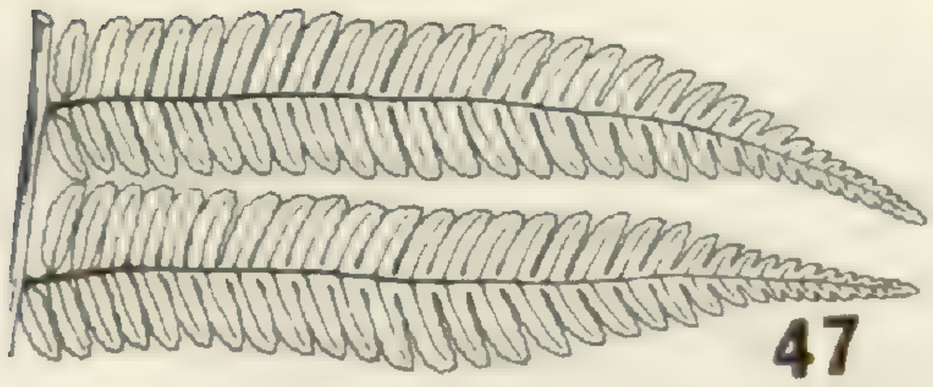
ADDITIONAL SPECIMENS EXAMINED: **Cuba. Oriente:** *Clément 782* (GH), *1350, 5233* (US), *1654* (F), *1661* (UC), *1672* (M,US); *Eggers 5252* (US); *Ekman 3218, 3681* (S), *5388* (NY,S,US); *Hioram 6989, 6999, 7291, 7295, 7306* (US); *Hioram & Clément 6380, 6381, 6384, 6387* (US); *Hioram & Maurel 2420, 4094, 6033* (US); *León 11089, 12638*

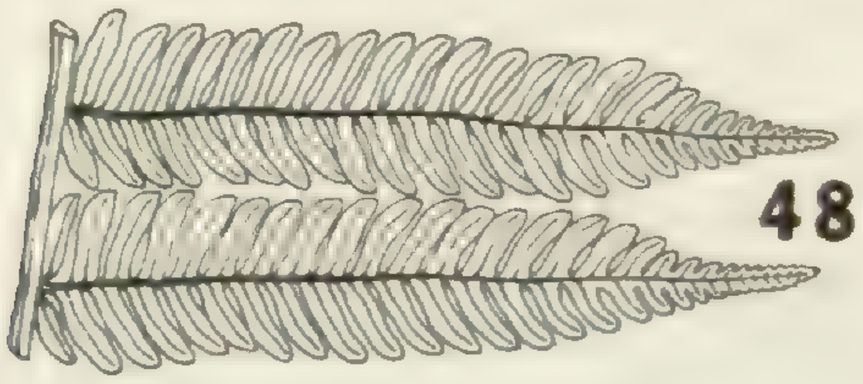
(NY,US); *León & Chateauvieux 3897* (NY); *León & Maurel 3804* (NY); *León et al. 10216* (NY); *Maxon 4105* (GH,NY,UC,US), *4206* (GH,M,NY,US), *4226* (NY,US), *4264* (F,GH,NY,US); *Morton 9292, 9435* (US); *Morton & Acuna 3620* (GH,NY,UC,US); *Pollard & Palmer 153* (F,GH,MO,NY,US); *Shafer 7999* (GH,NY,US), *8714* (GH,MO,NY,US); *Taylor 449* (NY,US); *Underwood & Earle 641* (NY), *644* (NY,US); *Wright 892, 1832* (GH), *948* (F,GH,US), *951* (US), *3930, 3932* (GH,NY,US), *3931* (GH,NY). **Las Villas** (formerly Santa Clara): *Britton & Britton 5106* (F,NY,US); *Dressler 1322* (MO); *Ekman 18515* (NY,S); *Hodge & Howard 4758* (MO); *Howard 5223, 6567* (GH,NY), *5290* (GH,MO), *5319* (GH,MO,NY); *Jack 6988* (GH,NY), *7002, 7023, 7241* (F,GH,NY), *7020* (GH,NY,US), *7117* (F,GH,UC), *7231* (F,GH,MO,NY,US); *León & Clément 3989* (NY pro parte), *8108* (US); *León & Roca 8104, 8108* (NY); *Morton 4239* (GH,MO,NY,UC,US); *Roig & Acuna 6125* (NY). **Pinar del Rio:** *Ekman 10673* (US); *León 12638* (NY,US), *12929* (MO,NY), *14140* (NY); *Morton 4327* (MO,US), *4373* (M,US); *Roig & León 6398* (NY).











FIGS. 42–44. Nephelea woodwardioides var. woodwardioides: 42, Central pinnules of a central pinna, *Maxon* 9557 (NY), × 0.5; 43, Central portion of a pinnule in 45, × 2; 44, Abaxial view of pinna-rachis showing conspicuous dark pneumatodes at costa axils, *Hart* [US 830481], × 2. FIGS. 45–47. Nephelea woodwardioides var. cubensis: 45, Central pinnules of a central pinna, *Morton & Acuna 3620* (GH), × 0.5; 46, Central portion of a pinnule in 45, × 2; 47, Central pinnules of a central pinna, variant coriaceous form with more closely spaced segments, a longer tapering pinnule apex, and at most sub-bullate scales on the abaxial costule surface, *Taylor 449* (NY), × 0.5. FIGS. 48, 49. Nephelea woodwardioides var. Hieronymi: 48, Central pinnules of a central pinna, *Gastony et al. 203* (GH), × 0.5; 49, Central portion of a pinnule in 48, × 2.

7c. **Nephelea woodwardioides** var. **Hieronymi** (Brause) Gastony, comb. et stat. nov.

FIGS. 48, 49, MAP 10

Cyathea Hieronymi Brause, in Urban Symb. Ant. 7: 152. 1911. TYPE: Santo Domingo (Dominican Republic), prope Constanza, 1200 m. alt., in fissuris montium humidis, Mart., 1910, *H. von Türckheim* 2992, presumably at B (not seen); isotypes: F!,GH!,M!,MO!,NY!,P!,US!

Nephelea Hieronymi (Brause) Tryon, Contrib. Gray Herb. 200: 40. 1970.

Adventitious buds on the stems of some specimens. *Unexpanded croziers* with blackish spines to 15 mm. long and brown scales with a dark apical seta to 0.25 mm. long. *Petiole* to ca. 0.5 m. long stramineous to brown, with blackish spines to 14 mm. long, the scales on the abaxial surface few. *Lamina* rigidly papyraceous to subcoriaceous, the apex more or less gradually acute, abruptly reduced and pinna-like. *Rachis* stramineous to brown. *Central pinnae* sessile to short (to ca. 1 cm.) petiolulate, narrowly ovate-lanceolate, to 63 cm. long and 19 cm. wide; *basal pinnae* quite reduced, to ca. 25 cm. long; *pinna-rachis* abaxially furfuraceous and with occasional blackish centered scales ca. 1.2 mm. long, pubescent distally with mostly inconspicuous lateral pneumatodes at costa axils. *Pinnules* sessile to short (to ca. 1.5 mm.) petiolulate, narrowly ovate to narrowly triangular; *costa* adaxially pubescent, glabrescent distally, abaxially furfuraceous-squamose, pubescent distally, the scales with black to blackish-brown centers. *Segments* sub-falcate to falcate with lateral margins entire to serrate-crenate, apex subentire to serrate-crenate; *costule* adaxially occasionally pubescent distally and with apically dark-setate bullate to sub-bullate scales.

Among the varieties of *Nephelea woodwardioides*, the spines on the croziers and petioles reach their greatest development in var. *Hieronymi*. This is the only variety where evidence of adventitious buds on the stem has been observed. In *Gastony et al. 156*, these buds gave rise to six branches at 0.3–0.5 m. above the ground and probably arose when apical dominance was broken by the previous decapitation of the main stem at 4 m. The maximum diameter of this stem was 30 cm. in the region of the adventitious root sheath; above the adventitious roots and below the persistent petiole bases the stem diameter was only 10 cm.

Variety *Hieronymi* is endemic to Hispaniola where it is fairly common and its range is quite extensive at ca. 300–1850 m. (especially above 800 m.). It occurs on calcareous and lateritic soils of mossy cloud forest and rain forest in partial to well-shaded situations, on mountain slopes and in ravines and sink holes.

ADDITIONAL SPECIMENS EXAMINED: **Dominican Republic. Duarte** (formerly Pacificador): *Abbot 2031* (GH pro parte, NY,US). **San Cristobal** (formerly Santo Domingo): *Allard 14304* (US); *Ekman H11501* (F,NY,S,US). **La Vega:** *Allard 13488* (NY,US); *Gastony et al. 156, 203* (GH,NY,US). **Peravia** (formerly Azua): *Ekman H11912* (S,US). **Puerto Plata:** *Ekman H14290* (NY,US). **Azua:** *Ekman H6344* (S,US). **Santiago Rodriguez** (formerly Monte Cristi): *Ekman H12699* (S). **San Juan:** *Howard 9441* (GH,NY,US). **Barahona:** *Abbott 1666* (F,GH,NY,US); *Howard 12323* (GH,NY). **San Rafael-Independencia:** *Gastony et al. 435* (GH,NY,US). **Haiti. Nord:** *Nash & Taylor 1743* (NY,US). **Ouest:** *Buch 1135, 1551* (US); *Ekman H1291* (F,GH,S,US), *H1764* (US), *H3227* (S,US); *Holdridge 2051* (F,NY); *Leonard 3814* (GH,NY,US), *5356* (US); *Proctor 10799* (US).

8. **Nephelea Tussacii** (Desv.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

Figs. 50–52, Map 11

Cyathea Tussacii Desv. Mém. Soc. Linn. Paris **6**: 323. 1827. (= Prod. 323. 1827). TYPE: Jamaica, *De Tussac,* P (not seen), photos GH!, UC!, US!. Another sheet at P! with this name and "In Jamaica," Herb. Desvaux is taken as an isotype.

Cyathea Tussacii var. *magnifolia* Jenm. Bull. Misc. Inform. Roy. Bot. Gard. Trinidad **3** (15): 53. 1898. (= West Ind. and Guiana Ferns, 53). TYPE: Jamaica, very abundant in forests 4,000–6,000 ft. alt., chiefly in damp gloomy ravines, probably *Jenman,* probably TRIN or K (not seen); possible isotypes: NY!.

Stem to 8 m. tall and 10 cm. in diameter, bearing brown to tan scales especially toward the apex and blackish spines to 12 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 11 mm. long and with brown to tan scales with a dark apical seta 0.25 mm. or less long and without lateral setae. *Petiole* to 1 m. long, brown to grayish-brown with blackish spines to 10 mm. long, the scales on the abaxial surface sparingly persistent, brown, some with a darker central stripe, with a single dark apical seta to 0.25 mm. (usually less) long and without lateral setae. *Lamina* rigidly papyraceous to sub-coriaceous, to ca. 3 m. long and 1.6 m. wide, tripinnate (predominately bipinnate-pinnatifid), with a gradually acute apex. *Rachis* light brown, adaxially furfuraceous-pubescent and often squamose, some scales with lateral and apical setae, abaxially furfuraceous-squamose, the deciduous larger scales leaving a sub-spinose, scabrous surface. *Central pinnae* mostly sessile or sub-sessile to short (to ca. 1 cm.) petiolulate, narrowly ovate-lanceolate, to 70 cm. long and 23 cm. wide; *basal pinnae* not highly reduced, to ca. 36 cm. long; *pinna-rachis* adaxially pubescent and more or less squamose with long, narrow, tan scales, abaxially furfuraceous-squamose, the larger scales leaving a scabrous base when deciduous, with mostly inconspicuous lateral pneumatodes at costa axils, not greenish-alate between the more distal sessile pinnules. *Pinnules* to ca. 14 cm. long and 3 cm. wide, deeply pinnatifid (pinnate at the base), sessile, elliptic to triangular, the apex acuminate; *costa* adaxially pubescent, abaxially pubescent, or distally so, and squamose, the scales mostly tan, (the larger ones with a brownish central stripe) to 2–3 mm. long, flat to bullate and usually with a single dark apical seta (occasionally more), occasionally with scales clustered in the axil. *Segments* sub-falcate to falcate with lateral margins and apex entire to crenulate, (basal segments often lobate), margins slightly revolute; *costule* adaxially glabrous or occasionally with one to few stiff trichomes distally, abaxially pubescent and with dark-setate to non-setate bullate to sub-bullate scales; *veins* once (rarely more) forked at or near the costule, evident on both surfaces or sometimes adaxially obscure, adaxially (when mature) and abaxially glabrous; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the forking of the veins; *indusium* cyathiform to urceolate, brown, of firm texture, persistent and usually entire at maturity, glabrous (obscurely squamuliferous when immature); *receptacle* globose to columnar, inserted to slightly exserted, with short (to ca. 0.2 mm. long) paraphyses, occasionally tufted at the apex of the receptacle.

There are six sheets of *Cyathea Tussacii* var. *magnifolia* at NY in the Jenman herbarium which bear his label "Type specimen—collected 1874–1879." The status of these specimens as isotypes cannot be determined. They are considered to be possible isotypes because they are in the Jenman herbarium and bear the varietal epithet in Jenman's hand, not because of Jenman's "Type specimen" labels. These labels are irrelevant to and should not be considered in typification, since there are several instances in which collections clearly without relevance to the nomenclatural type bear such labels (e.g., five sheets at NY and one at US annotated by Jenman as *C. Tussacii* Desv.).

The combination of indusial type and strongly squamose axes abaxially makes *Nephelea Tussacii* a very distinctive species. Jenman (1898) noted that it drops all its leaves in the dry season. Its affinities with *N. concinna* are discussed under that species.

Nephelea Tussacii is endemic to the Blue Mountains of Jamaica where it occurs in mossy cloud forest or on shaded wet slopes and in moist ravines at altitudes of ca. 750–1650 m.

ADDITIONAL SPECIMENS EXAMINED: **Jamaica. Portland:** *Gastony 21* (GH); *Hatch 7, 9* (UC,US); *Maxon & Killip 1288* (F,GH,NY,US); *Moore & Read 9559* (GH); 1932, *Papenfuss* (UC,US); *Proctor 5210* (MO,US), *5712* (MO). **Portland-St. Thomas:** *Maxon 9805* (GH,NY,US); *Maxon & Killip 1191* (F,GH,NY,US). **St. Thomas:** *Hatch 13* (US). **Portland-St. Andrew:** *Chrysler 1687* (MO). **St. Andrew:** *Campbell 7724* (F,NY,US); *Clute 164* (NY,US); *Hart 33* (US); *Maxon 1043* (US); *Underwood 1528* (NY,US), *2166* (NY).

9. **Nephelea concinna** (Jenm.) Tryon, Contrib. Gray Herb. 200: 38. 1970.

FIGS. 53–57, MAP 12

Cyathea arborea var. *concinna* Bak. ex Jenm. Jour. Bot. **19**: 52. 1881. TYPE: Jamaica, 1879, *Jenman 2*, K!

Cyathea concinna (Jenm.) Jenm. Bull. Dept. Jam. **26**: 4. 1891.

Stem to 6 m. tall and 6.5 cm. in diameter (20 cm. in diameter including the investing sheath of adventitious roots), bearing brown scales especially toward the apex and blackish spines to 6 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 10 mm. long and brown scales with a dark apical seta 0.25 mm. or less long and without lateral setae. *Petiole* to 0.4 m. long, dark brown to grayish-brown with blackish spines to 9 mm. long, the scales on the abaxial surface usually sparse to few, rather uniformly brown with a dark apical seta to 0.1–0.2 mm. long and without lateral setae. *Lamina* papyraceous to rigidly papyraceous, to ca. 2.5 m. long and 0.95 m. wide, bipinnate-pinnatilobate to bipinnate-pinnatifid, with a gradually acute apex. *Rachis* brown, adaxially pubescent-squamose to glabrescent, abaxially furfuraceous to glabrescent. *Central pinnae* sessile to short (to ca. 0.5 cm.) petiolulate, narrowly ovate-lanceolate, to ca. 45 cm. long and 10 cm. wide; *basal pinnae* more or less reduced, to ca. 10 cm. long; *pinna-rachis* adaxially pubescent and more or less squamose with long narrow tan to brown scales, abaxially squamose-furfuraceous to glabrescent, pubescent distally, with usually inconspicuous lateral pneumatodes at costa axils, not alate between the most distal sessile pinnules. *Pinnules* to ca. 5.5 cm. long and 1 cm. wide, pinnatifid, sessile to sub-sessile, narrowly elliptic to irregular in shape, usually more or less strongly contracted in fertile regions, the apex more or less acute to blunt; *costa* adaxially sparsely pubescent to glabrescent, abaxially pubescent or distally so and squamose, the scales tan to brown, mostly bullate to sub-bullate, usually with one to few dark apical setae, occasionally clustered in the axil. *Segments* (variously suppressed in the fertile region where the pinnule may be merely crenate to lobate) straight to sub-falcate with lateral margins entire to crenate, apex crenulate, margins slightly or not revolute; *costule* adaxially glabrous or with one to few stiff trichomes distally, abaxially pubescent and occasionally with one or more dark-setate or non-setate bullate scales proximally; *veins* mostly simple, occasionally forked, evident on both surfaces, adaxially glabrous, abaxially glabrous or with an occasional trichome; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the forking of the veins or at or near the costule on simple veins; *indusium* cyathiform to urceolate, brown, of firm texture, persistent and usually entire at maturity, glabrous; *receptacle* globose to occasionally columnar, inserted to slightly exserted, with short (to ca. 0.2 mm. long) paraphyses, occasionally tufted at the apex of the receptacle.

A sheet of *Cyathea arborea* var. *concinna* at NY! in the Jenman herbarium and bearing his "Type specimen" label is probably not part of the same collection as the holotype at K, although it is an authentic representative of the name. A specimen at P! in the Hart herbarium annotated as *C. concinna,* presumably by Jenman and referred to by him in a note on the type sheet at K, is probably not part of the type series either.

The status of *Nephelea concinna* as a species appears to be somewhat questionable. It is certainly very closely related to *N. Tussacii,* from which it is usually best distinguished by the size and degree of complexity of the leaf. Given that the leaf of *N. concinna* is smaller and less complex than that of *N. Tussacii* (maximally bipinnate-pinnatifid versus tripinnate), it is not unexpected that its veins are also less branched and that the indument characters associated with axes of higher orders in the more complex leaves tend to be shifted toward axes of lower order in the more simple leaves (cf., major heading separating these species in the key). The irregular appearance of the partially contracted fertile pinnules found throughout the leaves of *N. concinna* suggests a teratological condition. This is quite similar to the condition found elsewhere in highly fertile leaves where the fertility extends to the very distal pinnae which are transitional to a lower degree of complexity than that predominant in the leaf. At least one collection I have seen *(Gastony 24)* would certainly be placed in *N. Tussacii* on the basis of its stem, croziers, and indument characters, were it not for the size and complexity of its leaves. Another point of congruity between these two taxa is their uniqueness among the Jamaican Cyatheaceae in reportedly dropping all their leaves in the dry season (Jenman, 1898). It might be suggested that what is called *N. concinna* is simply a form of *N. Tussacii* produced by ecologic catastrophes such as exposure resulting from landslides or exceptionally stressing dry periods. I have observed in the field and collected portions *(Gastony & Gastony 951)* of a large perfectly healthy fertile specimen, however, which grew among other tree ferns in a quite undisturbed habitat.

The spores and sporangia of *Nephelea concinna* appear quite normally developed, but it is possible that *N. concinna* is a hybrid between *N. pubescens* and *N. Tussacii. Nephelea pubescens* has the least degree of laminal complexity in the genus and might contribute to the lesser laminal complexity and diminutive basal pinnae of *N. concinna* when compared to *N. Tussacii.* Hybridity could also account for the teratological-like aspect of the fertile pinnules of *N. concinna.* All three taxa are sympatric and endemic to the Blue Mountains of Jamaica. Until field population studies and related laboratory investigations of these taxa can be made, however, it seems best to maintain them as distinct species recognizable by the distinguishing characters indicated here and in the key to species.

Nephelea concinna is endemic to the Blue Mountains of Jamaica where it occurs in cloud forest and rain forest on ridges and slopes and in ravines at altitudes of ca. 1065–1675 m.

ADDITIONAL SPECIMENS EXAMINED: **Jamaica.** *Hart 166* (US). **Portland:** *Fisher 95* (NY); *Gastony 24* (GH); *Gastony & Gastony 951* (GH); 1919, *Pessin* (US); *Riba 198* (GH). **Portland-St. Thomas:** *Maxon 10039* (GH,NY,US). **Portland-St. Andrew:** *Chrysler 1659* (US); *Maxon 1576* (US); *Underwood 2635* (NY). **St. Andrew:** *Harris 7721* (US); *Proctor 6691* (US); *Underwood 1532* (NY,US); *Watt 12* (US).

10. **Nephelea setosa** (Kaulf.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

FIGS. 58–61, MAP 13

Alsophila setosa Kaulf. Enum. Fil. 249. 1824. TYPE: Brazil, *Chamisso*, presumably destroyed at LZ; isotype: B!.

Hemitelia setosa (Kaulf.) Mett. Fil. Lechl. **2**:30. 1859.

Cyathea setosa (Kaulf.) Domin, Pterid. 264. 1929.

Cyathea Beyrichiana Presl ex Hook. Icon. Pl. **7**: t. 623. 1844 and Sp. Fil. 1: 21. 1844. (Presl, Tent. Pterid. 55. 1836. nom. nud.). Isosyntypes: Brazil: *Sellow* P!, HBG photos UC!, US!; *Beyrich* P!, L photos NY!, US!; Rio de Janeiro, *Gardner 135* BM!. I am not choosing a lectotype because I have not examined the materials at Kew that Hooker saw.

Hemitelia Beryichiana (Hook.) Presl, Gefässbündel Stipes der Farrn, 45. 1947 (preprint from Abhandl. böhm. Ges. V, 5:353. 1848).

Amphicosmia Beryichiana (Hook.) Moore, Ind. Fil. civ. 1857.

Lophosoria dorsalis Fée, Crypt. Vasc. Brésil. 1:173. 1869. TYPE: In Brasilia fluminensi, in loco v. d. Novo Friburgo, ad ripas rivulorum, *Glaziou 2287*, P! in herb. Cosson; isotypes: P!, S!, US!.

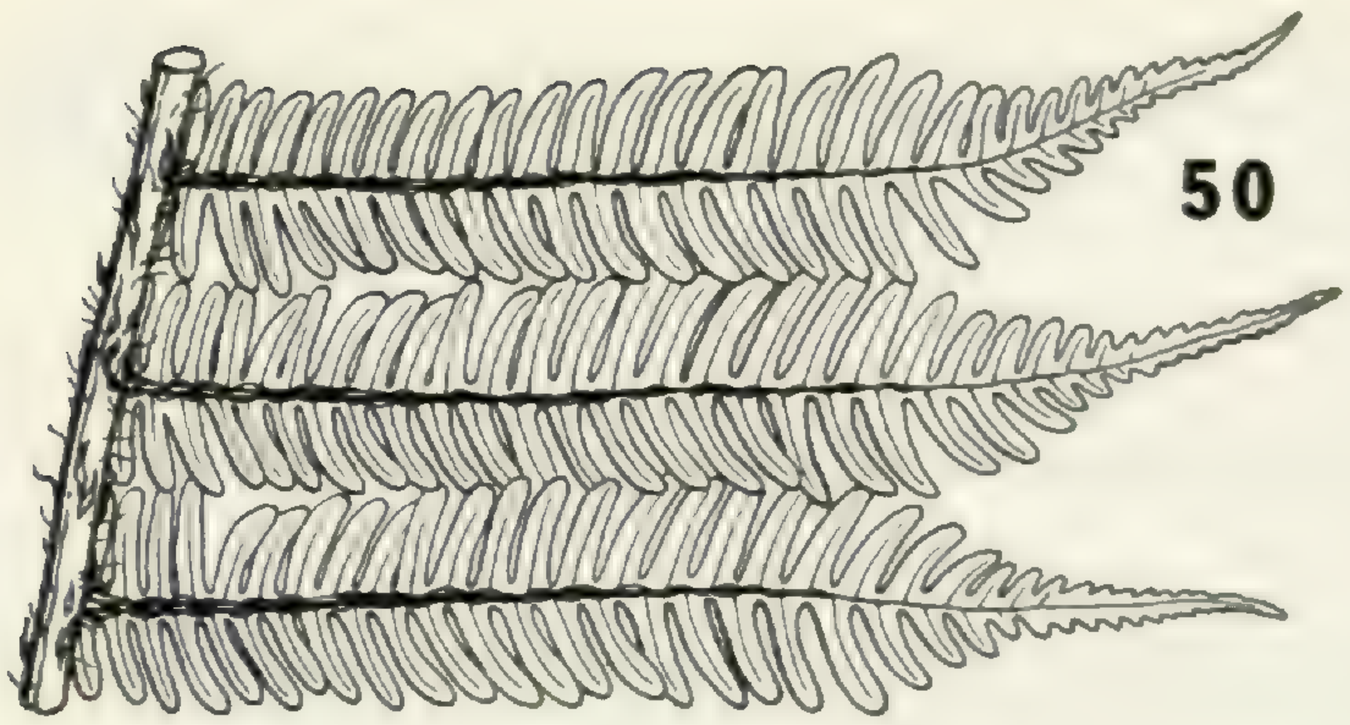
Alsophila dorsalis (Fée) Christ, Bull. Herb. Boiss. II, **2**:648. 1902.

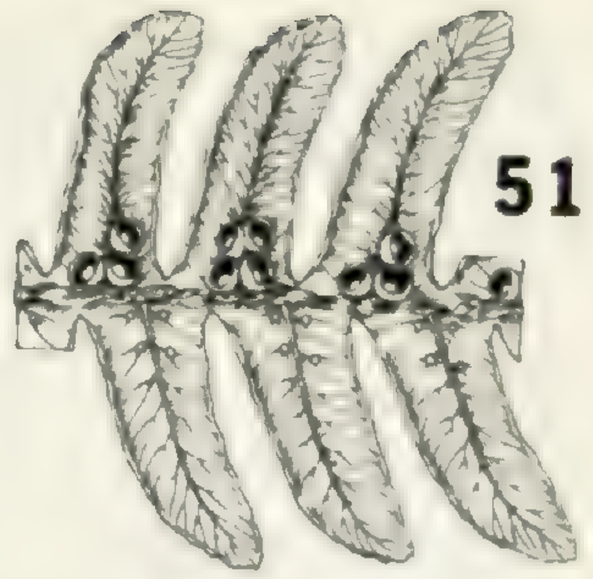
Cyathea dorsalis (Fée) Domin, Pterid. 262. 1929.

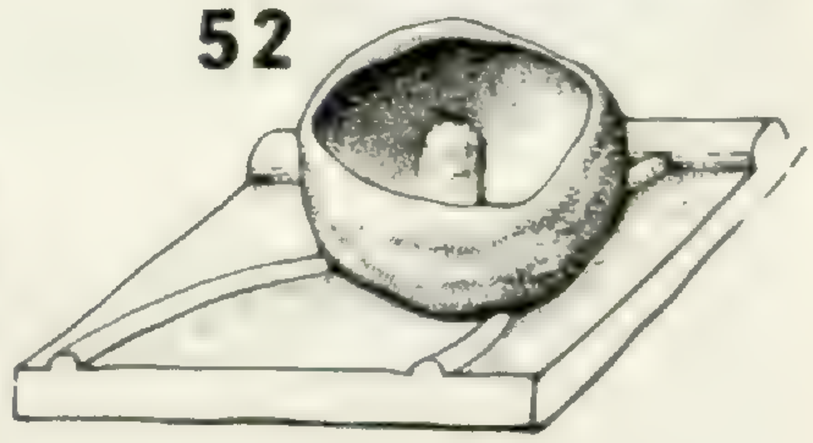
Cyathea leucosticta Fée, Crypt. Vasc. Brésil. **1**. 182. 1869. TYPE: In Brasilia fluminensi, Tijuca, *Glaziou 1700*. P! in herb. Casson; isotypes: fragment in herb. Jeanpert F!, fragment ex Fée NY!

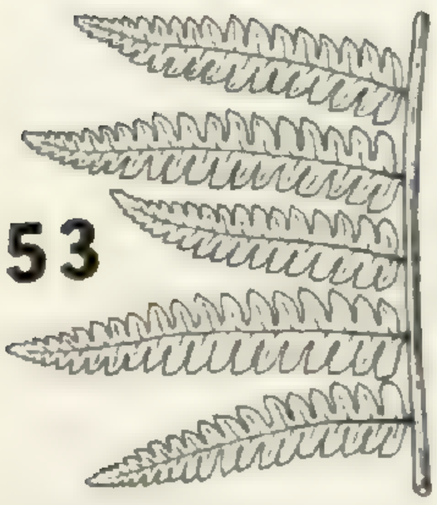
Hemitelia setosa var. *crenata* Rosenst. Hedwigia **46**:64. 1906. TYPE: Brazil, Santa Catarina, Lages, Colonia Annita Garibaldi, *Spannagel 134*, presumably S-PA (not seen); isotype: US!

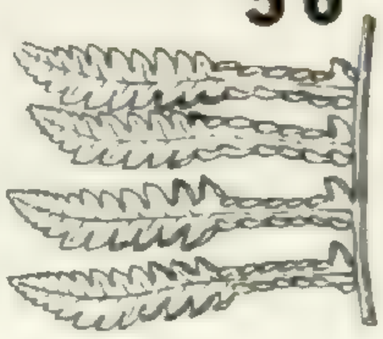
Stem to 10 m. tall and 10 cm. in diameter, scales not seen, bearing blackish spines (length uncertain), occasionally with adventitious buds. *Unexpanded croziers* not seen. *Petiole* to ca. 0.05–0.15 m. long to the sub-aphlebioid basal pinnae, light brown, with blackish spines to 4 mm. long, the scales on the abaxial surface usually numerous, occasionally deciduous, tan to brown, usually with a dark brown central stripe, with a dark apical seta to 0.5–1.0 mm. long and often with smaller additional apical and lateral setae. *Lamina* rigidly papyraceous to sub-coriaceous, length not known, to ca. 1.2 m. wide, tripinnate (predominately bipinnate-pinnatifid) usually abruptly reduced to a more or less distinct pinna-like apex (to 35 cm. long). *Rachis* light brown, adaxially pubescent, abaxially furfuraceous-glabrescent; *central pinnae* sessile to ca. 3.5 cm. petiolulate, ovate-lanceolate, to ca. 64 cm. long and 20 cm. wide; *basal pinnae* highly reduced, often to 7–12 cm. long and sub-aphlebioid in structure; *pinna-rachis* adaxially pubescent, abaxially furfuraceous to mostly glabrescent, pubescent distally, with usually inconspicuous lateral pneumatodes at costa axils, occasionally greenish-alate between the more distal sessile pinnules. *Pinnules* to ca. 10 cm. long and 2 cm. wide, deeply pinnatifid (often pinnate at the base), sessile to short (to ca. 2 mm.) petiolulate, ovate, the apex acute to acuminate; *costa* adaxially pubescent, abaxially sparsely squamose to furfuraceous-glabrescent and pubescent or distally so, the scales not significantly clustered in the axil. *Segments* sub-falcate with lateral margins crenate to crenulate, (occasionally subentire), apex crenulate-serrulate, margins usually slightly revolute; *costule* adaxially glabrous or with one to several stiff trichomes distally, abaxially pubescent and with occasional squamules to ca. 0.5–0.75 mm. long, often with numerous trichomoid processes and with or without dark setae; *veins* once (occasionally more) forked at or near the costule, evident on both surfaces,

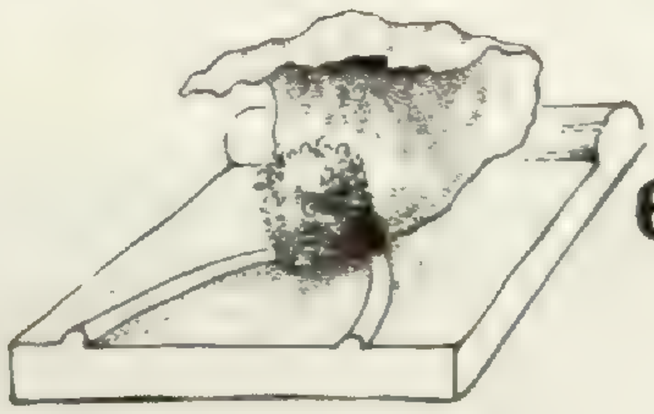












FIGS. 50–52. Nephelea Tussacii: 50, Central pinnules of a central pinna, *Maxon & Killip 1191* (GH), × 0.5; 51, Central portion of a pinnule in 50, × 1.5; 52, A representative cyathiform indusium, sporangia not shown, as in 50, × 15. FIGS. 53–57. Nephelea concinna: 53, Central pinnules of a sterile central pinna, with adjacent pinnules of unequal length, *Maxon 10039* (US), × 0.5; 54, Partially fertile pinnule of a central pinna, *Underwood 2365* (NY), × 0.5; 55, Fertile pinnule portion from a central pinna, unusual in its uncontracted and non-revolute segments, as in 54, × 2; 56, Representative fertile pinnules of a central pinna, the fertile segments contracted and strongly revolute, *Underwood 1532* (US), × 0.5; 57, Portion of a fertile pinnule in 56, × 2. FIGS. 58–61. Nephelea setosa: 58, Central pinnules of a central pinna, *Smith & Brade 2201* (GH), × 0.5; 59, Central portion of a pinnule in 58, × 2; 60, A hemitelioid indusium attached only to the side of the receptacle toward the costule, sporangia not shown, as in 58, × 15; 61, A sub-aphlebioid basal pinna attached to the rachis, *Jürgens 64* (S), × 0.5. The diminutive size of the pinna and its skeletonized lamina surface are also representative of the sub-aphlebioid basal pinna condition in N. pubescens and N. Grevilleana. FIGS. 62, 63. Nephelea Tryoniana: 62, Central pinnules of a central pinna, *Steyermark 30009* (US), × 0.5; 63, Central portion of a pinnule in 62, × 2.

adaxially glabrous, abaxially glabrous or with an occasional stiff trichome; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the primary forking of the veins; *indusium* hemitelioid, tan to light brown, of more or less delicate texture, persistent, glabrous; *receptacle* columnar to globose, with more or less conspicuous to inconspicuous short (to 0.2–0.3 mm. long) paraphyses.

Tryon (1971, p. 18) has discussed the evidence suggesting that the Fée tree fern specimens in the Cosson Herbarium at P are types. A sheet at P! has been annotated by Christ as a new species of *Cyathea* with an epithet honoring the collector (Brazil, Paraná, Ponta Grossa in sivula, 12 XII 1908, *P. Dusén 3219*), but this name apparently was never published.

Because of its sub-aphlebioid basal pinnae and hemitelioid indusia, *Nephelea setosa* is one of the most distinctive species in the genus. It is unique in its indusial type and shares the basal pinnae condition only with *N. pubescens* and *N. Grevilleana*. In these two characters, it is reminiscent of *Alsophila capensis* (L.f.) J. Sm. and is considered to be primitive. Its relations to other species of *Nephelea* are not clear. As in several other species of *Nephelea*, it occasionally shows a tendency toward dimorphism in the lamina contraction of its fertile pinnae and rarely has pinnules which disarticulate from the pinna-rachis, at least with drying.

Nephelea setosa occurs in southeastern Brazil in the states of Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, in the Misiones province of Argentina, and in the Sierra de Amabay in Paraguay. It is frequently found at low altitudes of ca. 20–1300 m. in ravines, campos and shady forests.

ADDITIONAL SPECIMENS EXAMINED: **Brazil. Rio de Janeiro:** *Brade 10018, 10610* (R), *Glaziou 980* (BM,US); *I.G. 99* (R); *Lima 21* (R); *Lutz 2051* (R); *Sampaio 2055* (R,UC,US); *Sick 8* (HB); *Smith & Brade 2201* (F,GH,UC,US). **São Paulo:** 1913, *Brade* (R). *5824* (SP); *Eiten et al. 2149* (NY,US); *Gerdes 97* (UC); *Leite 3565* (A); *Luederwaldt 1197* (UC), *6619, 6621* (SP); 1925, *Lutz* (R); *Wacket 79* (UC). **Paraná:** *Dusén 3219* (P), *6764* (F,GH,MO,S), *14839* (S,US); *Schwacke 82* (R). **Santa Catarina:** *Luederwaldt 6620* (SP); *Müller 163* (R); *Reitz 1149* (R,S,US). **Rio Grande do Sul:** *Brauner 120* (F,HB); *Glaziou 319* (US); *Jürgens 64* (A,F,MO,S,UC,US), *Jürgens 68* (UC); *Leite 696* (NY); *Lindman 1123* (S,US); *Sehnem 1314* (US). **Argentina. Misiones:** *de la Sota & Cuezzo 1432* (F,HB); *Meyer 11834* (GH); *Rodriguez 414* (GH). **Paraguay.** *Shering 6622* (SP). **Amambay:** *Rojas 10428* (MO,NY,UC).

2416

11. **Nephelea Tryoniana** Gastony, sp. nov.

FIGS. 62, 63, MAP 14

Caulis ad 4.5 m. altus, diametro 15 cm. (vaginam investientem radicum adventitiarum includens), spinis nigellis ad 11 mm. longis et praesertim apicem versus squamis brunneis fulvisve praeditus, gemmis adventitiis incognitis. *Crozieres* non-evolutae non visae. *Petiolus* ad 0.4 m. longus, pallide brunneus, spinis nigellis ad 7 mm. longis instructus, squamae pagina abaxiali sparsae, fulvae brunneaeve margine pallidae apice setiferae (seta fuscata, ad 0.5 mm. longa) et saepe alias setas minores apice margineque ferentes. *Lamina* papyracea, longitudine ignota, ad 1.3 m. lata, raro tripinnata (plerumque bipinnata-pinnatifida) apicem versus gradatim acuta. *Rachis* pallide brunnea, adaxialiter pubescens-squamosa, abaxialiter furfuracea-scabrida praesertim proximaliter. *Pinnae centrales* sessiles vel sub-sessiles, anguste

ovatae, ad 63 cm. longae et 16 cm. latae; *pinnae basales* non valde deminutae, ad 30 cm. longae (breviter petiolulatae); *rachis pinnae* adaxialiter pubescens (squamis longis fulvis sparsim intermixtis), abaxialiter squamosa furfuraceaque (saepe scabrida post lapsum squamarum majorum), distaliter pubescens squamosaque squamis bullatis, pneumatodiis lateralibus ad axillam costae inconspicuis, sine alis viridulis inter pinnulas sessiles distallissimas. *Pinnulae* ad 8 cm. longae et 1.5 cm. latae, valde pinnatifidae (interdum basi vix pinnatae), sessiles vel breviter (ad 3 mm.) petiolulatae, anguste ovatae, apicem versus plerumque acuminatae vel acutae; *costa* adaxialiter pubescens, raro squamis paucis intermixtis, abaxialiter pubescens et squamis planis vel sub-bullatis albis-fulvescentibus apice margineque setiferis (setis fuscatis) instructa, squamis distalioribus bullatis et setis fuscatis carentibus, plerumque squamis ad axillam fasciculatis. *Segmenta* recta vel sub-falcata, marginibus lateralibus integra vel subintegra, apice integra vel serrulata, marginibus leviter revolutis; *costula* adaxialiter trichomatibus rigidis distaliter, abaxialiter squamulis bullatis vel sub-bullatis, squamulis costularibus similibus, praedita et plerumque sparsim pubescens (raro glabrescens); *venae* ad propeve costulam semel furcatae, in paginis ambabus conspicuae, adaxialiter abaxialiterque glabrae (raro abaxialiter trichoma rigidum ferens); *pagina* adaxialiter abaxialiterque inter venas glabra. *Sori* ad furcam venarum; *indusium* deficiens; *receptaculum* columnare vel globosum, paraphysibus plerumque inconspicuis brevibus (ad ca. 0.25 mm. longis) praeditum.

✓TYPE: Guatemala, Dept. Zacapa: pine-covered cañons bordering Río Lima, Sierra de las Minas, below Finca Alejandria, alt. 2000 m., Oct. 14, 1939, *J. A. Steyermark 30009* F! consisting of six sheets (*F1054354, 1054356, 1054405, 1054409, 1054412, 1054418*), one sheet (*F1054409*) now at GH; isotype: US!

Nephelea Tryoniana is unique in the genus in its lack of an indusium and is also distinctive in the copious and very characteristic flat to bullate scales found abaxially on its axes. Although I have not seen the croziers, I am confident that they bear conspicuous black spines because of the highly spinose nature of other parts (e.g., stem portions of *Steyermark 29925* and *30009*).

Although *Nephelea mexicana* and *N. polystichoides*, also from Central America, may at times appear to lack an indusium, critical examination will show remnants of their delicate, sphaeropteroid to sub-sphaeropteroid indusium at the base of the receptacle. Sterile material can readily be distinguished from *N. mexicana* and *N. polystichoides* by the projections bearing the larger scales on the abaxial pinna-rachis which leave a scabrous surface when the scales fall or are eroded, and by the bullate scales present abaxially on the costule and distal costa. Such bullate scales are not found in other species of *Nephelea* outside of the Greater Antilles. Their presence in this Central American species and the form of the lamina apex in this species (discussed above under Morphology and Anatomy) suggest that it may be a relict member of a group once common to the Greater Antilles and the region of Guatemala, Honduras, and Nicaragua. The former land connection between these areas from the Mesozoic through the upper Miocene-lower Pliocene (varying in extent and with a brief break in the upper Oligocene—Schuchert, 1935), may have influenced this distribution.

I am pleased to name this species for my mentor, Dr. Rolla M. Tryon, in recognition of his outstanding contribution to the understanding of the systematics and evolution of the family Cyatheaceae.

Nephelea Tryoniana is found in pine-covered canyons, cloud forest ravines and dense, wet, mixed mountain forest in Guatemala, Nicaragua and Honduras at altitudes of 1500–2500 m.

ADDITIONAL SPECIMENS EXAMINED: **Guatemala. Alta Verapaz:** *Standley 90730* (US). **Zacapa:** *Steyermark 29925* (F). **Honduras. Francisco Marazan:** *Carlson 2661, 2662* (F). **Nicaragua. Matagalpa:** *Molina 20369* (GH).

12. **Nephelea erinacea**
(Karst.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

Stem to 12 m. tall and 15 cm. in diameter (including the investing sheath of adventitious roots), bearing tan to brownish scales especially toward the apex and blackish spines to 10 mm. long, occasionally with adventitious buds. *Unexpanded croziers* with blackish spines to 13 mm. long and tan to brown scales with a dark apical seta to 1.0 mm. long (many to only ca. 0.25 mm.) and without lateral setae. *Petiole* to 1.2 m. long, brown to purple-brown with blackish spines to 15 mm. long, the scales on the abaxial surface copious, brown to whitish-tan with or without a darker central stripe, with a dark apical seta to 0.25–0.5 mm. long and without lateral setae. *Lamina* coriaceous, to 3 m. long and ca. 1.6–2.0 m. wide, (rarely partially tripinnate) predominately bipinnate-pinnatifid, usually abruptly reduced to a distinct pinna-like apex (to ca. 60 cm. long). *Rachis* brown to purple-brown, adaxially minutely pubescent (occasionally slightly furfuraceous) to glabrescent, abaxially furfuraceous to glabrescent. *Central pinnae* sessile to short (to ca. 1–2 cm.) petiolulate, elliptic-lanceolate or ovate-lanceolate to narrowly so, to 104 cm. long and 30 cm. wide; *basal pinnae* not highly reduced, to ca. 20–40 cm. long; *pinna-rachis* adaxially pubescent, abaxially furfuraceous-glabrescent to more or less pubescent with crispate trichomes, the latter especially distally, with inconspicuous to often swollen and conspicuous lateral pneumatodes at costa axils, not greenish-alate between the most distal sessile pinnules. *Pinnules* to ca. 15.5 cm. long and 3 cm. wide, deeply pinnatifid (the basal segments often free on the basiscopic side with the acroscopic side adnate; basal segments only rarely truly sessile or free), sessile to subsessile, occasionally short (to ca. 1 mm.) petiolulate, narrowly ovate to narrowly triangular, the apex acute to acuminate (rarely caudate); *costa* adaxially pubescent, abaxially furfuraceous-squamose to glabrescent, sparsely pubescent distally, the scales mostly small and variously darkened, occasionally concolorous with their several dark setae, occasionally clustered in the axil. *Segments* falcate to sub-falcate, with lateral margins entire to crenulate, apex entire to subentire, margins not revolute to highly so; *costule* adaxially glabrous or infrequently with one to few stiff trichomes distally, abaxially with dark-setate squamules like those of the costa but smaller (to ca. 0.5 mm. long) and occasionally with one to few stiff trichomes distally; *veins* once-forked at or near the costule (rarely twice-forked) evident on both surfaces or occasionally adaxially obscure, adaxially glabrous or with occasional minute whitish stellate squamules (ca. 0.2–0.3 mm. in diameter) especially near the segment margins, abaxially with occasional minute whitish stellate squamules (ca. 0.25 mm. in diameter) with a variable number of irregular processes and sometimes with a diminishing continuation of the small dark-setate squamules of the costule; *lamina surface* adaxially and abaxially glabrous between the veins, except usually with minute whitish trichomoid squamules at or near the margins. *Sori* at the primary forking of the veins; *indusium* cyathiform to urceolate or rarely sub-sphaeropteroid, brown to dark brown, of more or less firm texture, persistent, frequently ruptured at maturity into two to four lobes, glabrous to densely lepidote; *receptacle* globose to columnar, inserted to slightly exserted, with mostly inconspicuous, short (to ca. 0.2 mm. long) paraphyses.

This is a widespread species but the variability of its critical characters is slight making it easy to recognize. It is readily separated from *Nephelea cuspidata*, with which it has been confused most frequently, by its coriaceous lamina, by its occurance at higher altitudes, by the stellate squamules found abaxially on the veins (Fig. 67), by the pinna-rachis being non-alate between the more distal sessile pinnules, and especially by the presence of scales with only one dark apical seta and no lateral setae (Fig. 66) on the abaxial surface of the petiole base.

KEY TO VARIETIES

Indusia glabrescent to sparsely and obscurely lepidote. Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia. ..... 12a. var. *erinacea*.
Indusia densely and persistently lepidote, the scales often with dark setae. Ecuador. ..... 12b. var. *purpurascens*.

12a. **Nephelea erinacea** var. **erinacea**

FIGS. 64–67, MAP 15

Cyathea erinacea Karst. Linnaea **28**: 453. 1857. TYPE: Venezuela, Merida: crescit ad pedem australem montis glaciali Meridensi, alt. 2000 m., *Karsten*, probably LE or W (not seen); isotype: B! in herb. Mett.

16725 *Cyathea aureonitens* Christ, Bull. Herb. Boiss. II. 4:948. 1904. LECTOTYPE: *Pittier 2413*, Costa Rica, Cartago, Río Navarrito, 1400 m., BR! in herb. Christ; isolectotypes: NY! fragment ex B, P! Syntypes: *Wercklé 229* (not seen), *Wercklé* s.n. (specimen uncertain); isosyntypes: *Tonduz 13332* GH!, M!, NY!, NY! fragment ex B, US!; *Alfaro 16496* US! fragment ex herb. Rosenstock.

Nephelea aureonitens (Christ) Tryon. Contrib. Gray Herb. 200:40. 1970.

Cyathea cuspidata var. *rigida* Rosenst. Meded. Rijks Herb. Leiden **19**: 6. 1913. TYPE: Bolivia, Espritu Santo, in silvis udis montanis, 1600 m., Jun. 1911, *Herzog 2237*, L (not seen), fragment US!; isotypes: M!, S!, UC!, US!.

Stem to 12 m. tall and 15 cm. in diameter, bearing blackish spines to 10 mm. long, occasionally with adventitious buds. *Unexpanded croziers* with blackish spines to 13 mm. long and tan to brown scales with a dark apical seta to 1.0 mm. long (many to only ca. 0.25 mm.) and without lateral setae. *Petiole* to 1.2 m. long, brown to dark brown with blackish spines to 15 mm. long. *Lamina* to 2 m. wide, the apex usually abruptly reduced to a distinct pinna-like apex (to ca. 60 cm. long). *Rachis* brown to dark brown. *Central pinnae* ovate-lanceolate, to 104 cm. long and 30 cm. wide; *pinna-rachis* with often swollen and conspicuous lateral pneumatodes at costa axils. *Pinnules* sessile to sub-sessile, narrowly ovate to narrowly triangular, the apex acuminate (rarely caudate); *costa* furfuraceous-squamose to glabrescent abaxially and sparsely pubescent distally, when present the scales occasionally concolorous with their several dark setae. *Segments* with lateral margins entire to crenulate and slightly or not revolute. *Indusium* glabrous to sparsely and obscurely lepidote, the squamules more or less stellate and similar to those on the veins.

In the protologue of *Cyathea aureonitens*, Christ cited at least five collections: *Wercklé 229* and *s.n.*, *Alfaro 16496* at Capelladas, *Tonduz 13332* at Las Vueltas Tucurrique, and *Pittier 2413* at Río Navarrito 1400 m. I have seen Christ herbarium material of *Pittier 2413* (BR) and of two sheets of Wercklé without number in 1903 and 1904 respectively (P). The latter two are possible syntypes, but it cannot be determined if these are

the actual *Wercklé s.n.* sheets cited in the protologue. In 1969, Rolla Tryon found at P both a Wercklé and an Alfaro collection passing under the Herb. Nac. Costa Rica number 16496. Christ confused the numbers *Tonduz 13332* and *1332* (see discussion below under *Cyathea basilaris*). I have chosen *Pittier 2413* as lectotype because I have seen the sheet in the Christ herbarium and because of the confusion associated with the other collections.

As in several other species of *Nephelea,* the pinnules often disarticulate from the pinna-rachis. The leaves are often borne in apparent whorls of four or five (the former giving the stem a squarish cross section).

Variety *erinacea* occurs in the mountains of Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, and Bolivia in wet ravines and on sparsely to heavily wooded slopes in cloud forest or rain forest at altitudes of ca. 700–2500 m. (predominantly above 1400 m.).

ADDITIONAL SPECIMENS EXAMINED: **Costa Rica.** *Jiménez 1099* (US); *Kupper 1471* (M). **Alajuela:** *Scamman 7581* (GH,US); *White & Lucansky 196825* (DUKE,GH). **Guanacaste:** *Brener 15546* (F). **Heredia:** *Chrysler & Roever 5613* (MO,UC); *Nisman 48, 109* (GH). **San José:** *Brade 94* (UC), *Brade under Rosenstock 108* (A,M,MO,UC); *Gastony & Gastony 753, 763, 765, 767* (GH); *Nisman 23* (GH), *42* (GH Sheet 1); *Scamman 7580* (F,GH,NY,UC,US); *Scamman & Holdridge 7856, 7858* (GH); *Stork 1384* (UC); *Wercklé,* Herb. Jim. no. *562, 583* (US), Herb. Nac. Costa Rica no. *16416* (NY,US); *White & Lucansky 1968121, 1968127* (DUKE,GH). **Cartago:** *Alfaro 8072* (GH,NY,US); *Nisman 125, 152, 165* (GU); *Scamman 7014* (GH); *Standley & Torres 51230* (GH,US); *Tryon & Tryon 7039* (GH); *Wercklé,* Herb. Nac. Costa Rica no. *16750* (US); *White & Lucansky 196833, 196834, 196835, 196836, 196858, 196861, 196892, 196893, 196895, 196898, 1968111, 1968148, 1968170, 1968171, 1968192* (DUKE,GH); *L. O. Williams 19787* (US). **Puntarenas:** *Nisman 147, 158* (GH). **Panama. Chiriqui:** *Cornman 1227* (MO,UC,US), *1228* (US), *1229* (MO,UC); *Killip 5072* (GH,US); *Maxon 5575* (GH,NY,US). **Venezuela. Merida:** *White & Lucansky 1969244a, 1969245* (DUKE,GH). ***Colombia.*** *Lindig 283* (GH). **Magdalena:** *H. H. Smith 2222* (GH,NY). **Santander:** *Killip & Smith 19267* (GH,NY,US). **Antioquia:** *Daniel 1214* (US); *Hodge 6828* (GH, US). **Cundinamarca:** *Amórtegui 285* (US); *Garcia-Barriga 12560, 12567* (US); *Little & Little 8574* (GH, US). **Cauca:** *Dryander 2903* (F pro parte), *2907* (F). **Ecuador. Napo-Pastaza:** *Sydow 895* (BM,US). **Pichincha:** *Solis 5822* (F). **Tungurahua:** *Prescott & Wiggins 20* (US). **Santiago-Zamora:** *Dodson & Thien 1443* (MO,US). **El Oro:** *Steyermark 53766* (F, US). **Peru. Amazonas:** *Hutchison & Wright 6803* (GH,UC). **Huanúco:** *Macbride 4843* (F,US). **Bolivia. Yungas:** *Rusby 121* (US). **Cochabamba:** *Steinbach 9478* (F,GH,MO, UC,US).

12b. **Nephelea erinacea** var. **purpurascens** (Sod.) Gastony, comb. et stat. nov.

FIGS. 68, 69, MAP 16

Cyathea purpurascens Sod. Crypt. Vasc. Quit. 503. 1893. TYPE: Ecuador, Imbabura: crece en los bosques occidentales del volcán Cotacachi cerca de hacienda Quisaya, 1900 m., *Sodiro s. n.* A sheet at P! leg. *Sodiro* 2/1874 with duplicates ex herb. P at A! (two sheets) and MO!, and a sheet at NY! leg. 4/1874 are all authentic from "Cotacachi prope Quisaya" and may be type material. Before a lectotype sheet is chosen, the Sodiro collection supposedly at Q should be consulted.

Nephelea purpurascens (Sod.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

Cyathea oxyacantha Sod. Sert. Fl. Ecuad. II, 6. 1908. TYPE: Ecuador, Pichincha: crescit in silvis suband. vulc. Atacatzo, *Sodiro s.n.*, possible holotype P! (leg. *Sodiro* 3/1906); isotype: US! ex Rosenstock.

Stem (ex descr.) to 2–3 m. tall and 12–15 cm. in diameter, bearing blackish spines of unknown length, adventitious buds not known. *Unexpanded croziers* not seen. *Petiole* to 0.6 m. long (ex descr.), brown to purple-brown with blackish spines to 7 mm. long. *Lamina* to 1.6 m. wide (ex descr.), the apex not known. *Rachis* dark brown to purple-brown. *Central pinnae* narrowly elliptic-lanceolate to narrowly ovate-lanceolate, to 70 cm. long and 20 cm. wide; *pinna-rachis* with mostly inconspicuous lateral pneumatodes at costa axils. *Pinnules* sessile to sub-sessile, occasionally short (to ca. 1 mm.) petiolulate, narrowly triangular, the apex acute to acuminate; *costa* furfuraceous-squamose abaxially and pubescent or distally so, the scales frequently concolorous with their several dark setae. *Segments* with lateral margins entire to subentire, rarely crenulate, and slightly to highly revolute. *Indusium* densely and persistently lepidote (except where eroded), the squamules more or less stellate and often dark setate.

Variety *purpurascens* is known only from the adjacent provinces of Imbabura and Pichincha in Ecuador where it occurs in wet forests on the slopes of a few volcanos at altitudes of (1900–) 2600–2800 m. It has apparently been derived from variety *erinacea* or their common ancestral form in the high altitude isolation of these Ecuadorean volcanos.

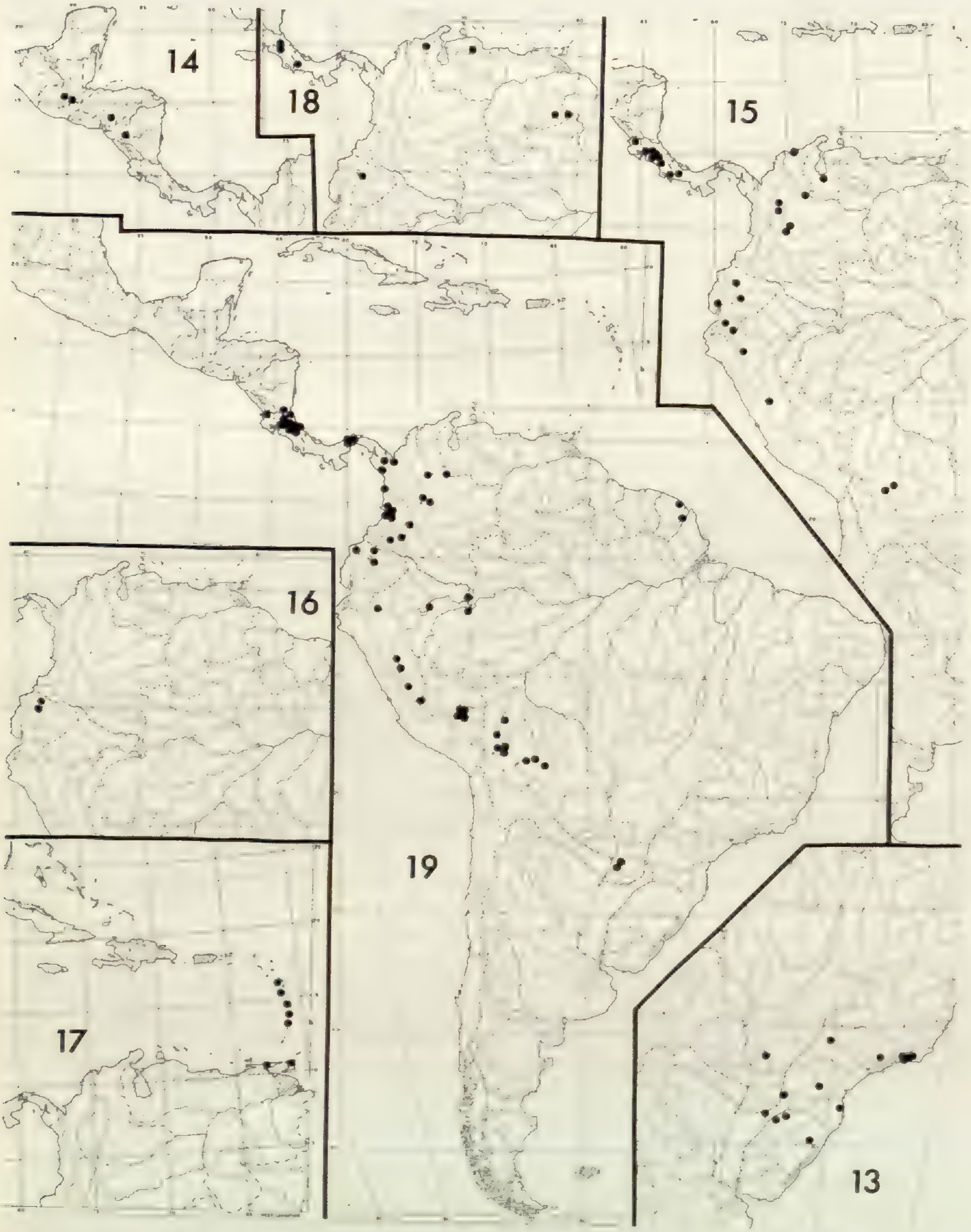
ADDITIONAL SPECIMENS EXAMINED: **Ecuador. Pichincha:** *Mille 170* (US), *s. n.* (NY,UC,US); 1900, *Sodiro* (US), 1907, *Sodiro* (NY,P,US pro parte).

13. Nephelea Imrayana

(Hook.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

Stem to 10 m. tall and 45 cm. in diameter (including the investing sheath of adventitious roots), bearing light tan to brown scales especially toward the apex and blackish spines to 26 mm. (usually less) long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 17 mm. (usually less) long and light tan to brown scales with a dark apical seta to 0.25–1.0 mm. long and without lateral setae. *Petiole* to ca. 0.51–1.2 m. long, brown with blackish spines to ca. 14 mm. (usually less) long, the scales on the abaxial surface usually persistently dense and felt-like, tan, occasionally with a darker central stripe, with a dark apical seta to 0.5 mm. long and without lateral setae. *Lamina* papyraceous to rigidly papyraceous, to ca. 3 m. long and 1.6 m. wide, (rarely partially tripinnate) predominantly bipinnate-pinnatifid, abruptly reduced to a distinct pinna-like apex (to ca. 40 cm. long). *Rachis* brown to dark brown, adaxially squamose-pubescent to glabrescent, abaxially furfuraceous-squamose to glabrescent, the larger scales persistent or deciduous and often leaving a scabrous surface. *Central pinnae* sessile to short (to ca. 1.5 cm.) petiolulate, ovate-lanceolate, to 90 cm. long and 27 cm. wide; *basal pinnae* not highly reduced, to ca. 36 cm. long; *pinna-rachis* adaxially more or less pubescent and squamose with long, narrow, tan to brown scales, abaxially furfuraceous-squamose, often with scabrous projections where the larger scales have fallen, pubescent to glabrescent distally, with mostly inconspicuous lateral pneumatodes at costa axils, not greenish-alate between the most distal sessile pinnules. *Pinnules* to ca. 14 cm. long and 2.5 cm. wide, deeply pinnatifid (the basal segments often free on the basiscopic side with the acroscopic side adnate; basal segments only rarely truly sessile or free), sessile, narrowly ovate to narrowly triangular, the apex acute to acuminate; *costa* adaxially pubescent, abaxially more or less densely furfuraceous-squamose to pubescent distally, the scales to 2–3 mm. long, the larger ones tan, with or without a brown central stripe, to brown and with a (usually single) dark apical seta, often clustered in the axil. *Segments* sub-falcate to falcate, with lateral margins entire to subentire, rarely crenate, (basal segments often auriculate on the basiscopic side with the basiscopic margin often more or less crenate), apex subentire to crenulate, margins slightly or not revolute; *costule* adaxially glabrous or rarely with one to several stiff

trichomes distally, abaxially distally glabrescent or with stiff trichomes, proximally more or less squamose with squamules to ca. 0.5 mm. long bearing several prominent dark apical and lateral setae or lacking dark setae; *veins* once-forked at or near the costule, evident on both surfaces or sometimes adaxially obscure, adaxially and abaxially glabrous; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the forking of the veins; *indusium* sphaeropteroid, with or without an umbo, tan to light brown, of more or less delicate texture, mostly persistent but irregularly rupturing at maturity, glabrous; *receptacle* globose to short-columnar, inserted, with short (to ca. 0.2 mm. long) paraphyses occasionally tufted at the apex of the receptacle.



Maps 13–19. 13, Nephelea setosa; 14, N. Tryoniana; 15, N. erinacea var. erinacea; 16, N. erinacea var. purpurascens; 17, N. Imrayana var. Imrayana; 18, N. Imrayana var. basilaris; 19, N. cuspidata.

In addition to the characters mentioned in the key, the dullness of the abaxial lamina surface and the lack of whitish stellate trichomoid squamules at or near the segment margins (such as chracterize *Nephelea erinacea*), serve to distinguish this species.

In plants from Guadeloupe to St. Lucia, the rachis, pinna-rachis, and costa are abaxially more or less densely and persistently furfuraceous-squamose, whereas in plants from St. Vincent, Trinidad, and the continent the costule is less densely squamose abaxially and the larger scales on the abaxial surface of the rachis and pinna-rachis are not as persistent. In the specimens from St. Vincent southward, however, there usually are clear scars and epidermal emergences where the larger deciduous scales were once attached. In some specimens from Trinidad (e.g., *Broadway 9969, Britton et al. 2287*), Venezuela *(Wurdack 34117)*, Colombia *(Grant 10879)*, and Panama *(Maxon 5670)*, the pinna-rachis is rather persistently furfuraceous-squamose abaxially, although perhaps not always as densely so as in material from Guadeloupe to St. Lucia.

The number of veins in an ultimate segment is variable. However, the variation does not have a significant correlation with geography. Throughout the Lesser Antilles and into Venezuela *(Wurdack 34117; Aristeguieta & Pannier 1927)* and Colombia *(Grant 10879)* the specimens show trichomes abaxially on the costule, although these are absent or poorly developed in other material from Venezuela *(Steyermark 58989)* and in that from Panama *(Maxon 5670)* and Costa Rica.

From Guadeloupe to the Paria peninsula of Venezuela the squamules borne more or less distally on the abaxial costule surface have a relatively small body and several prominent dark setae at the apex and sides (Fig. 73), whereas elsewhere in Venezuela and westward into Central America these more distal squamules (or many of them) feature a conspicuously greater body area (Fig. 76) with the setae relatively less conspicuous and less numerous (many have a single seta at the apex and some lack dark setae altogther).

The lack of coordination among the several clinal morphological tendencies observed in this species does not facilitate the recognition of infra-specific taxa. The morphological divergence of the species toward each end of its range, however, warrants the recognition of two varieties which may best be distinguished as below. Their geographic separation occurs in Venezuela.

KEY TO VARIETIES

Abaxially on the costule the more distal squamules bearing several dark apical and lateral setae, most of the scale body bearing setae (Fig. 73); conspicuous trichomes present abaxially on the costule. Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Trinidad, Venezuela. . . . . 13a. var. *Imrayana*.

Abaxially on the costule the more distal squamules bearing one to few dark apical setae (rarely lacking dark setae), most of the scale body lacking the setae (Fig. 76);

conspicuous trichomes absent abaxially on the costule in Central American and some South American material. Venezuela, Colombia, Ecuador, Panama, Costa Rica. . . . . 13b. var. *basilaris*.

13a. **Nephelea Imrayana** var. **Imrayana**

Figs. 70–74, Map 17

Cyathea Imrayana Hook. Sp. Fil. 1: 18, t. 9, B. 1844. LECTOTYPE: Dominica, Couliaban Mountain, *Dr. Imray,* K (not seen), fragments NY! in herb. Jenman and in herb. Underwood ex K.

Alsophila nigra Jenm. Bull. Misc. Inform. Roy. Bot. Gard. Trinidad 3 (15): 38. 1898, (=West Ind. and Guiana Ferns, 38), not Mart. Icon. Pl. Crypt. Bras. 71, t. 30 f. 5, t. 47. 1834. TYPE: locality and collector unrecorded, TRIN!, photo GH!.

Cyathea caribea Jenm. Bull. Misc. Inform. Roy. Bot. Gard. Trinidad 3 (15): 57. 1898, (=West Ind. and Guiana Ferns, 57). LECTOTYPE: St. Vincent, collector and data unrecorded, NY in herb. Jenman (not seen), photo GH!.

Cyathea Imrayana var. *caribaea* (Jenm.) Proctor, Rhodora 63: 32. 1961.

Cyathea Purdiaeai Jenm. Bull. Misc. Inform. Roy. Bot. Gard. Trinidad 3 (15): 58. 1898, (=West Ind. and Guiana Ferns, 58). TYPE: Trinidad, Sept. 6, 1862, *Purdie,* on the heights of Aripo, TRIN!; isotypes: BM!, photo GH! of NY sheet, K!, NY!, US!, UC! fragment ex NY; probable isotype: TRIN!.

Stem to 15 cm. in diameter (probably including the investing sheath of adventitious roots), bearing blackish spines to 9 mm. long. *Unexpanded croziers* with blackish spines to 8 mm. long and light tan to brown scales with a dark apical seta to 0.25–1.0 mm. long and without lateral setae. *Petiole* to 0.51 m. long, with blackish spines to 4 mm. (usually less) long. *Lamina* length not known, to ca. 1.6 m. wide. *Rachis* abaxially furfuraceous-squamose to glabrescent, the larger scales persistent or deciduous and often leaving a scabrous surface. *Central pinnae* to ca. 83 cm. long and 27 cm. wide; *basal pinnae* not highly reduced, to ca. 36 cm. long; *pinna-rachis* abaxially pubescent distally. *Segments* with lateral margins entire to subentire; *costule* abaxially with stiff trichomes distally, proximally with squamules bearing several prominent dark apical and lateral setae. *Indusium* sphaeropteroid, usually with an umbo.

Hooker cited as *Cyathea Imrayana* collections of Dr. Imray in Dominica and Dr. Bancroft in Jamaica. Jenman explicitly limited the species to Dominica (excluding Jamaican materials) and so effectively chose the Imray Dominica collection as the lectotype (Jenman, 1898, p. 59). *Cyathea Imrayana* var. *subnudata* Hook., of Jamaica, is treated under dubious and excluded names.

In the herbarium of John Smith at BM! is an authentic early collection of *Cyathea caribaea* Jenm. collected on St. Vincent by Caley and bearing John Smith's apparently unpublished epithet in the genus *Cyathea* honoring the collector.

On a collection from St. Lucia *(Proctor 17765)*, it is noted that the leaves are borne "in whorls of five, expanding simultaneously." Similar apparently whorled leaf arrangements have been observed in *Nephelea erinacea* and other species in Central America.

Variety *Imrayana* occurs in Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Trinidad, and the Peninsula de Paria of Venezuela at altitudes of ca. 350–980 m. on mountain slopes in mossy forest, cloud forest, and rain forest.

ADDITIONAL SPECIMENS EXAMINED: **Guadeloupe:** *Bailey & Bailey 78* (US); *Duss 4131* (NY pro parte); 1895, *Duss 4323* (NY); 1897, *Duss 4323 (4156)* (US); *Duss 4355* (F,GH,US); *Husnot 269* (F), *400* (F,NY); *L'Herminier 178* (NY), *s.n.* (F,MO,US); *Maze 10132* (NY); 1824, *Perrotet* (NY); *Proctor 20040* (A,US); *Questel 3222, 3250* (US). **Dominica:** *Chambers 2692* (UC,US); *Eggers 532* (M,NY); *Hodge & Hodge 1669* (GH,NY,US), *1848* (GH,US); 1882, *Jenman* (NY); *Lloyd 169* (NY,US); *Wilbur et al. 8209* (NY). **Martinique:** *Belanger 60* (NY), *s.n.* (F), 1857, *s.n.* (F); 1884, *Duss 1604* (NY), 1880, *Duss 1606* (US), 1883, 1885, 1897, *Duss 1606* (4131) (NY pro parte); *Hahn 33* (GH,NY). **St. Lucia:** *Proctor 17765* (GH,US). **St. Vincent:** *Beard 1427* (F,GH,MO,S,US); *Caley s.n.* (BM); *Eggers 6816* (F,US); *Morton 5895, 6175* (US), *6234* (NY,UC,US); *Smith & Smith 962* (US), *s.n.* (GH). **Trinidad:** *Britton et al. 1360* (GH), *2287* (GH,US); *Broadway 6216* (F,GH,MO,S,US), *9969* (F,GH,TRIN,US); *Purdie 10* (TRIN); *Seifriz 3* (US). **Venezuela. Sucre:** *Steyermark 94812* (GH,NY,VEN).

13b. **Nephelea Imrayana** var. **basilaris** (Christ) Gastony, comb. et stat. nov.

FIGS. 75, 76, MAP 18

9256 *Cyathea basilaris* Christ, Bull. Herb. Boiss. II, 4:949. 1904. LECTOTYPE: Costa Rica, *Wercklé s.n.* in herb. Christ presumably at P (not seen); possible isolectotype: NY! ex herb. Christ (1903, *Wercklé*); authentic material: 1903, *Wercklé & Brune*, P!, 1901–1905, *Wercklé*, US!.

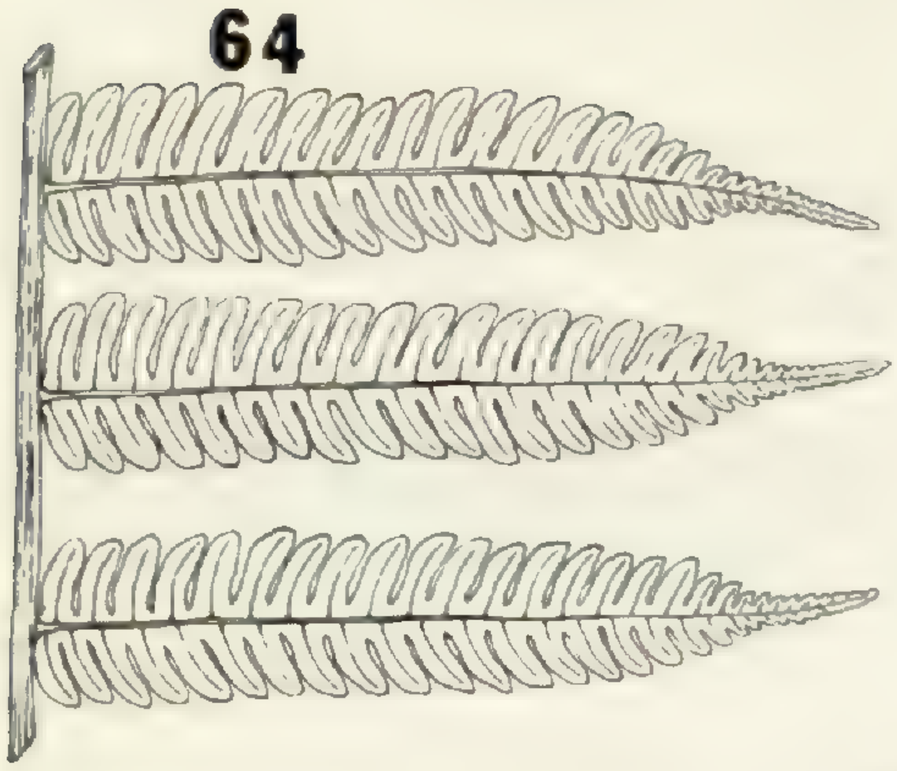
Nephelea basilaris (Christ) Tryon, Contrib. Gray Herb. 200:40. 1970.

Cyathea reticulata Wercklé ex Christ, Bull. Herb. Boiss. II, **5**: 251. 1905. TYPE: Costa Rica, Cartago: Irazú, 1800 m., *Wercklé 6*, P! in herb. Christ; isotypes: NY! fragment ex Christ, NY!, P!, US!.

Stem to 45 cm. in diameter (including the investing sheath of adventitious roots), bearing blackish spines to 26 mm. (usually less) long. *Unexpanded croziers* with blackish spines to 17 mm. long and light tan to brown scales with a dark apical seta to 0.5 mm. long and without lateral setae. *Petiole* to 1.2 m. long, with blackish spines to ca. 14 mm. (usually less) long. *Lamina* to ca. 3 m. long and 1.4 m. wide. *Rachis* abaxially slightly squamose to furfuraceous-glabrescent, sometimes scabrous where the larger scales have fallen. *Central pinnae* to ca. 90 cm. long and 25 cm. wide; *basal pinnae* condition not known; *pinna-rachis* abaxially not conspicuously pubescent distally. *Segments* with lateral margins entire to subentire, rarely crenate; *costule* abaxially glabrescent distally (occasionally with more or less stiff trichomes in South American material), proximally with squamules bearing one to few dark apical setae (rarely lacking dark setae). *Indusium* sphaeropteroid, umbo not observed.

In the protologue of *Cyathea basilaris*, Christ cited at least two collections: *Wercklé s.n.* and *Tonduz 1332*, forêts de las Vueltas Tucurrique, 1000 m. In his search for types in 1969, Rolla Tryon found in Christ's herbarium at P only two sheets under *C. basilaris: Tonduz 1332* and *Wercklé and Brune* in 1903. The Tonduz number is probably an error for 13332, as noted by Maxon on US sheet 74301. Because *Tonduz 13332* is *C. aureonitens* Christ, I follow Maxon and take the cited Wercklé collection as the lectotype of *C. basilaris* Christ. Unfortunately this sheet was not found in Christ's herbarium at P. The sheet in Christ's herbarium at P (*Wercklé and Brune* in 1903), however, is *C. basilaris* Christ and may be taken as authentic material.

A specimen with a stem diameter of 45 cm. *(Wurdack 34117)* from Estado Bolivar, Venezuela, represents the largest stem diameter recorded in the genus.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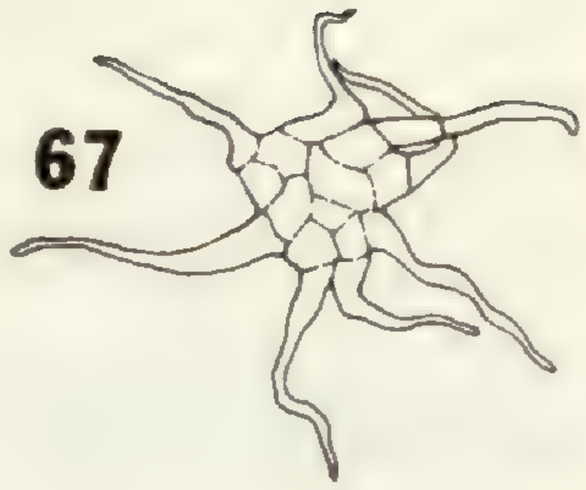
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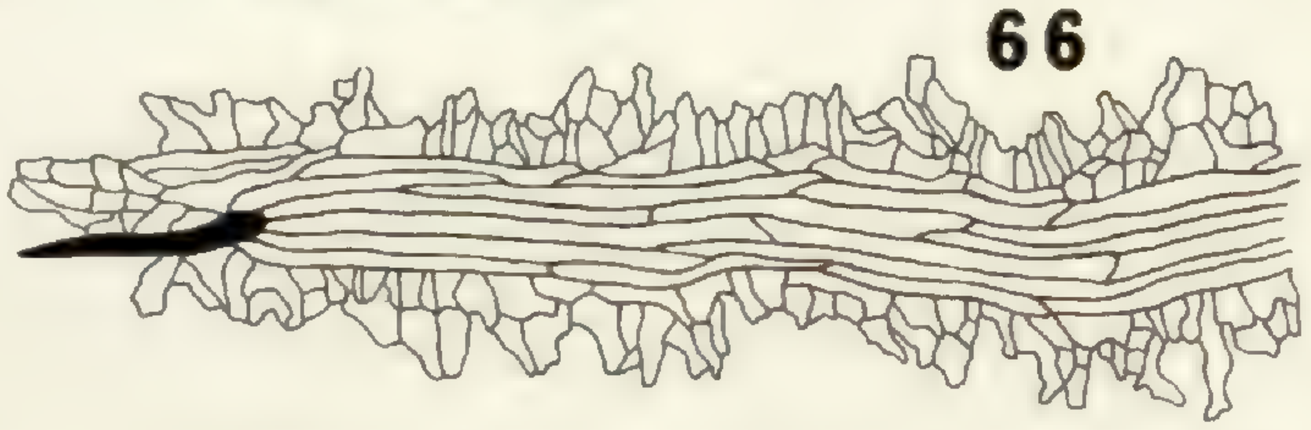
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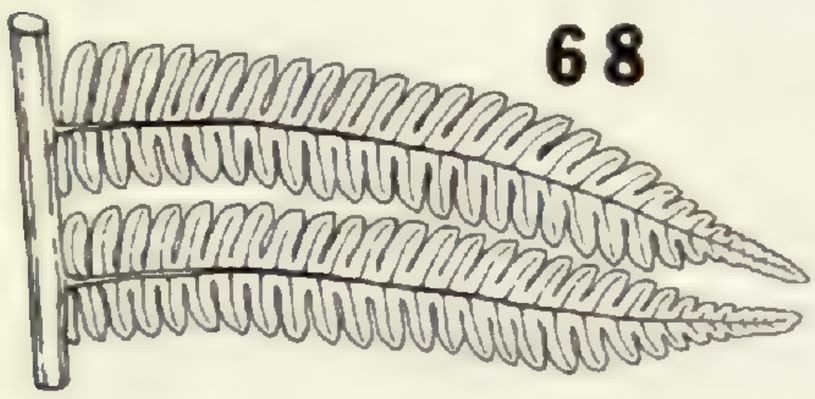
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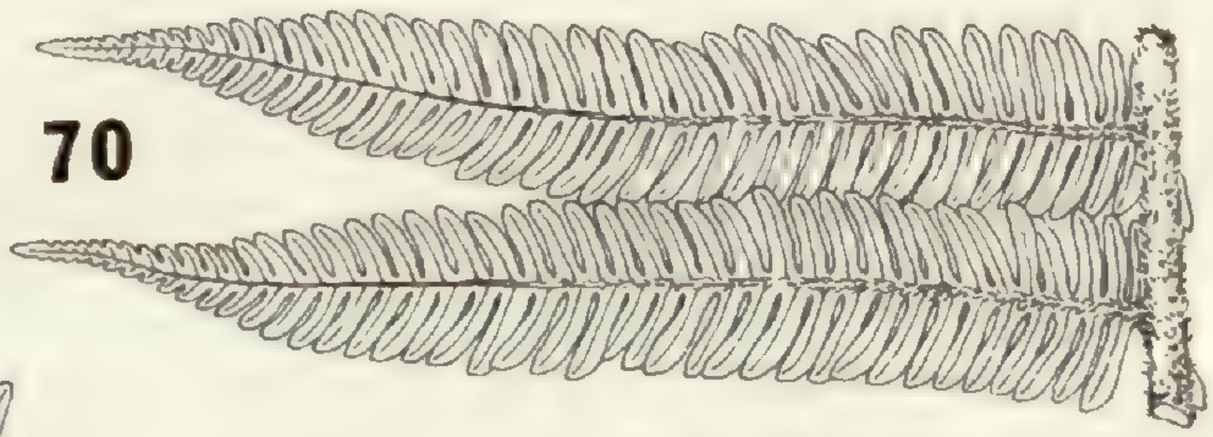
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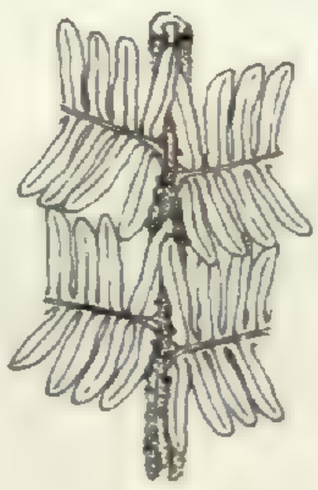
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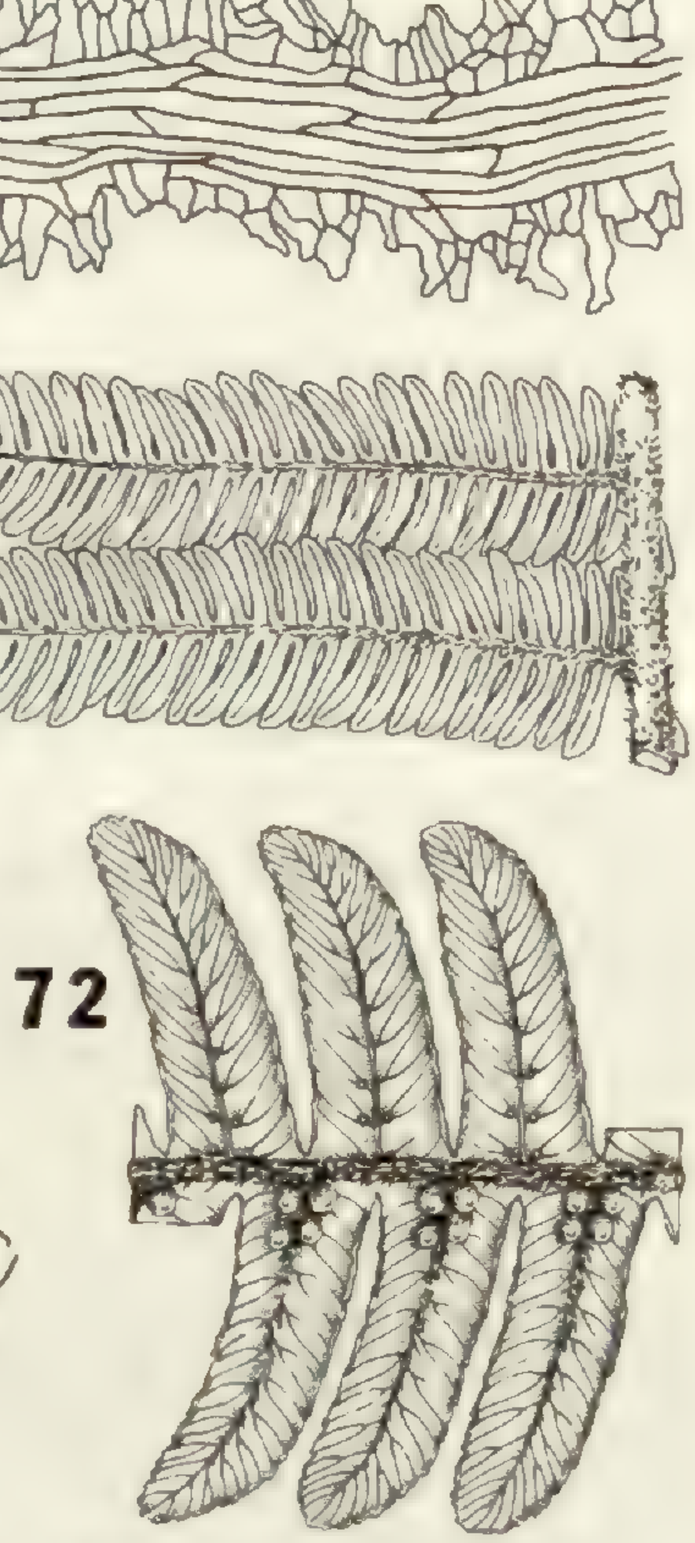
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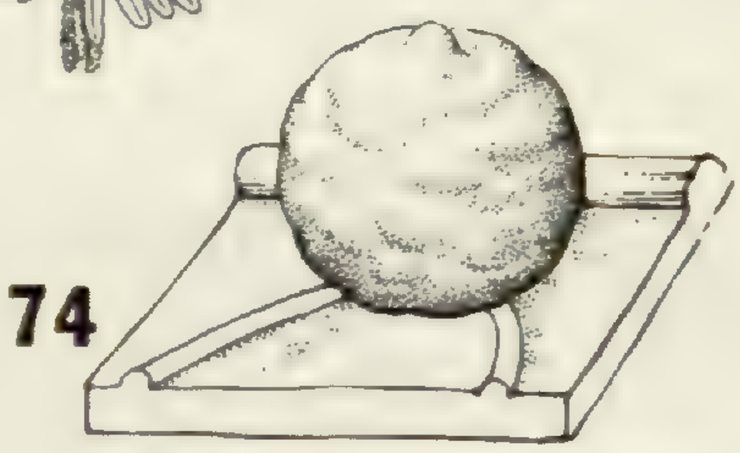
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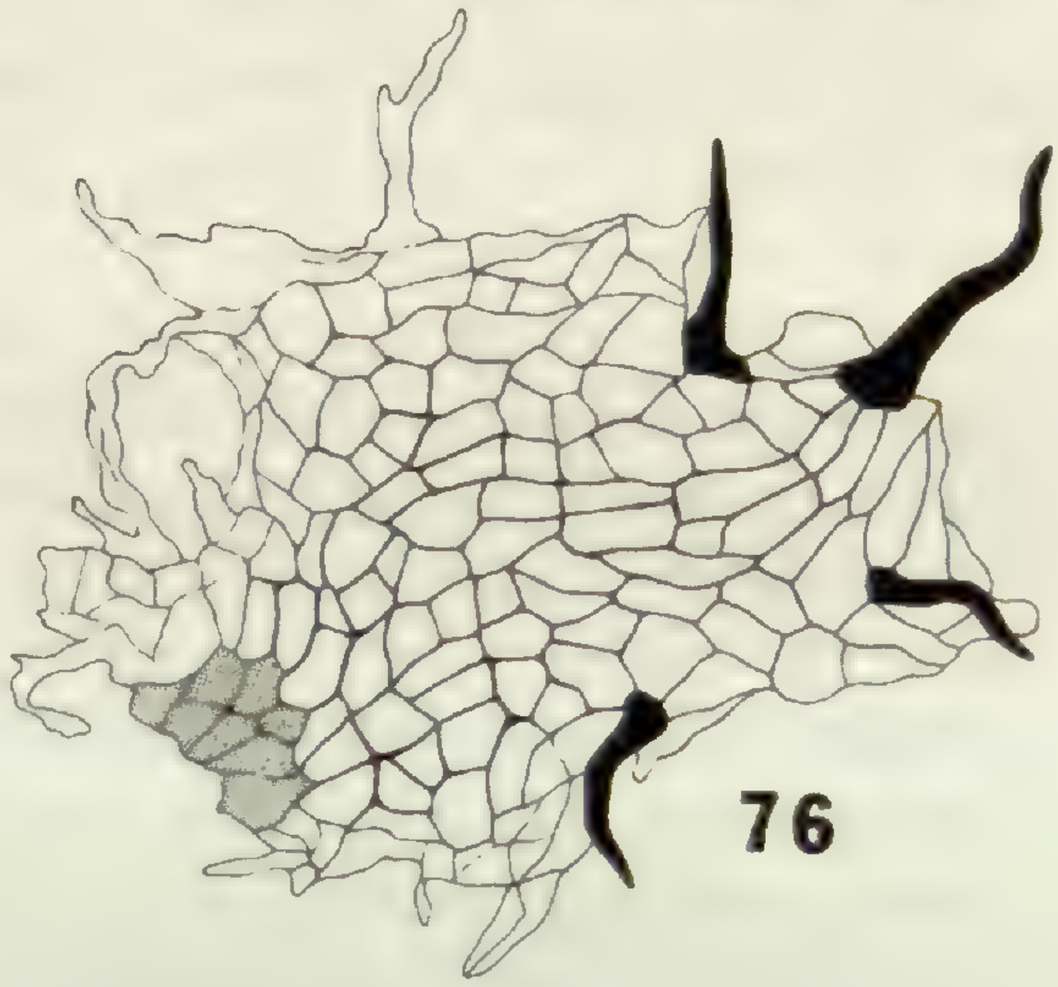
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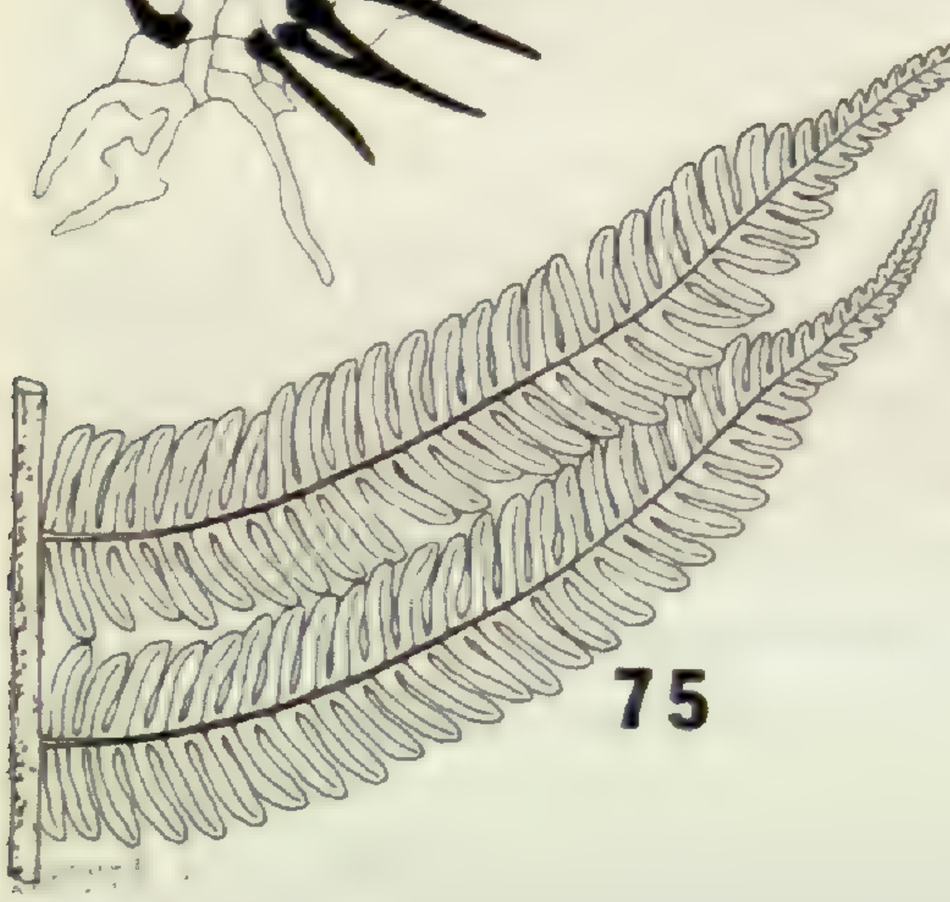

75

Variety *basilaris* is known from Venezuela, Colombia, Ecuador, Panama, and Costa Rica where it occurs at altitudes of ca. 1000–2250 m. in wet forests on ridges and mountain slopes.

ADDITIONAL SPECIMENS EXAMINED: **Venezuela. Bolivar:** *Steyermark* 58989 (GH, MO,NY,US); *Wurdack 34117* (GH,NY). **Yaracuy:** *Aristeguieta & Pannier* (US,VEN). **Colombia. Magdalena:** *Grant 10879* (US). **Ecuador. Napo-Pastaza:** *Grubb et al. 1334* (US). **Panama. Chiriquí:** *Maxon 5670* (US).

14. **Nephelea cuspidata** (Kze.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

FIGS. 77–80, MAP 19

Cyathea cuspidata Kze. Linnaea 9: 101. 1834. TYPE: Peru, prov. Maynas. crescit in sylvis paludosis, Febr., 1831, *Poeppig diar. 2286*, presumably destroyed at LZ; isotypes: B!, NY! fragments ex B and K, P!, US! fragment ex herb. Rosenstock.

Cyathea oyapoka Jenm. Bull. Misc. Inform. Roy. Bot. Gard. Trinidad 3 (15): 58. 1898, (=West Ind. and Guiana Ferns, 58). TYPE: Cayenne. French Guiana, in sylvis humidis ad torrentes Guyanae centralis Oyapok superior, Junio, 1833, *Leprieur*, NY in herb. Jenman (not seen), photo GH!; isotypes: F!, GH!, NY!, P! in herb. Cosson, US!, US! fragment ex herb. Br.-Guiana.

Cyathea punctifera Christ, in Pittier, Primit. Fl. Costaric. 3: 40. 1901. TYPE: Costa Rica, forêts de Tuís, 650 m., Nov. 1897, *Tonduz 11307*, BR (2 sheets, det. Christ)!; isotypes: GH!, NY! fragments ex BR and US, P! (two sheets, annotated as n. sp. Christ but not herb. Christ), US! six sheets, photo US! of BR sheet.

Cyathea Hassleriana Christ, Bull. Herb. Boiss. II, 7: 926. 1907. TYPE: Paraguay, La Cordillera: in silvis humidis pr. Caacupe, mens Sept., *Hassler 120*, presumably at P (not seen); isotype: S-PA! fragment in herb. Selim Birger ex Rosenstock.

Stem to 15 m. tall and 40 cm. in diameter (including the investing sheath of adventitious roots), bearing tan to brown scales especially toward the apex and blackish spines to 1 cm. long, occasionally with adventitious buds. *Unexpanded croziers* with (conspicuous to partially concealed) blackish spines to 11 mm. long and tan to brown scales with a dark apical seta to 0.5–1.0 mm. long and numerous smaller apical and lateral setae. *Petiole* to 0.5 m. long, brown, with blackish spines to 9 mm. long, the scales on the abaxial surface copious, tan to brown and with or without a darkened central stripe, with a dark apical seta to 0.5–1.0 mm. long and with usually numerous smaller apical and lateral setae. *Lamina* papyraceous, to 3 m. long and 1.5 m. wide, (very rarely partially tripinnate) predominantly bipinnate-pinnatifid, abruptly reduced to a distinct pinna-like apex (to 20–60 cm. long). *Rachis* brown (occasionally blackish-brown), adaxially minutely furfuraceous-pubescent to glabrescent, abaxially minutely furfuraceous to glabrescent. *Central pinnae* sessile

FIGS. 64–67. Nephelea erinacea var. erinacea: 64, Central pinnules of a central pinna, *Nisman 152* (GH), × 0.5; 65, Central portion of a pinnule as shown in 64, *Macbride 4843* (F), × 2; 66, Distal portion of a scale from the abaxial petiole surface, structurally marginate with a single dark apical seta and without lateral setae, *Gastony & Gastony 753* (GH), × 43; 67, A representative stellate squamule from the abaxial vein surface, with irregularly disposed processes, *Maxon 5575* (GH), × 85. FIGS. 68, 69. Nephelea erinacea var. purpurascens: 68, Central pinnules of a central pinna, Feb. 1874, *Sodiro* (P), × 0.5; 69, Central portion of a pinnule as shown in 68 from specimen at (A). FIGS. 70–74. Nephelea Imrayana var. Imrayana: 70, Central pinnules of a central pinna, *Chambers 2692* (US), × 0.5; 71, Adaxial view of basal portions of pinnules, with basal segments free and auriculate on the basiscopic side, as in 70; 72, Central portion of a pinnule as shown in 70, *Hodge 1669* (GH), × 2; 73, A squamule from the abaxial costule surface, with a relatively small body and several prominent dark setae, *Morton 6175* (US), × 85; 74, A representative unruptured sphaeropteroid indusium with an apical umbo, *Wilbur et al. 8209* (NY), × 15. FIGS. 75, 76. Nephelea Imrayana var. basilaris: 75, Central pinnules of a central pinna, *Steyermark 58989* (GH), × 0.5; 76, A squamule from the abaxial costule surface, with a conspicuously large body area and relatively inconspicuous dark setae, as in 75, × 85.

to short (to ca. 2 cm.) petiolulate, ovate-lanceolate, to 95 cm. long and 30 cm. wide; *basal pinnae* not highly reduced, to ca. 37–45 cm. long; *pinna-rachis* adaxially pubescent (rarely with scattered long, narrow, whitish-tan scales intermixed), abaxially minutely furfuraceous to glabrescent and pubescent distally, often with more or less persistent larger squamules along the sides which leave a scabrous projection when deciduous, with mostly inconspicuous to occasionally conspicuous lateral pneumatodes at costa axils, usually narrowly (ca. 0.2–0.5 mm. wide on each side) greenish-alate between the more distal sessile pinnules. *Pinnules* to 15 cm. long and 1.5–3.5 cm. wide, deeply pinnatifid (the basal segments often free on the basiscopic side with the acroscopic side adnate; basal segments only rarely truly sessile or free), sessile to short (to ca. 2 mm.) petiolulate, oblong, elliptic, or narrowly ovate, the apex more or less abruptly acuminate to caudate; *costa* adaxially pubescent, abaxially furfuraceous-squamose to pubescent distally, the scales mostly small with numerous dark setae, usually clustered in the axil. *Segments* sub-falcate to falcate with lateral margins entire or subentire to crenulate, apex subentire to crenulate; *costule* adaxially glabrous or with one to few stiff trichomes distally, abaxially with dark-setate squamules like those of the costa but smaller, often pubescent distally; *veins* once-forked at or near the costule or simple (rarely more than once-forked), evident on both surfaces, adaxially glabrous, abaxially with a diminishing continuation of the often sub-stellate indument of the costule and with sparse to frequent whitish stellate trichomes or highly trichomoid squamules with distinct, mostly rigid (sometimes dark) arms often 3–4 in number; *lamina surface* adaxially and abaxially glabrous between the veins, except often with whitish stellate trichomes at or near the margins. *Sori* at the forking of the veins; *indusium* urceolate (rarely cyathiform) to sphaeropteroid, lacking an apical umbo, light to usually dark brown, of firm texture, persistent and frequently rupturing at maturity into 2–4 lobes, bearing stellate indument similar to that on the veins or glabrescent; *receptacle* globose, inserted, with short (to ca. 0.1–0.2 mm. long) mostly quite inconspicuous paraphyses.

Although Maxon (1930) correctly associated Leprieur's number 267 with the type collection of *Cyathea oyapoka*, "in sylvis humidis ad torrentes Guayanae centralis Oyapok superior, Junio, 1833," there is at least one other collection of this taxon which bears the Leprieur number 267, viz., "in sylvis paludosis ad basin montium via Kaw, Guyane française, Leprieur 1847." The same number was evidently used for other collections of *Cyathea oyapoka*. Consequently the several sheets at F!, NY!, and US! which bear the number 267 without locality and date cannot unequivocally be designated isotypes. The sheets I have cited as isotypes are from the Leprieur herbarium and bear the locality and date of the type collection. Several of these and other sheets of this taxon collected by Leprieur are annotated with an apparently unpublished epithet in the genus *Cyathea* honoring the collector and attributed to Baker.

Underwood's label epithet "venusta" for a collection *(C. L. Smith 2033)* of *Nephelea cuspidata* from Nicaragua and that of Rosenstock, "pectinata," for a collection *(Brade 628)* from Costa Rica are both apparently unpublished.

Although it exhibits the greatest species range in the genus, *Nephelea cuspidata* is quite uniform in its critical characters and is easily recognized. Its most diagnostic features are the petiole and crozier scales which have several dark apical and lateral setae in addition to the main apical seta which is universal in the genus, the stellate trichomes found abaxially on the veins (Fig. 80), and the persistent, brown, firm, usually lobed and

often stellate-pubescent indusium. Its separation from *N. erinacea*, with which it has most frequently been confused, is facilitated by the first two of these characters. These features have been discussed under that species. It is adequately separated in the key from its closest relative, *N. sternbergii*.

The apparent disjunction in the range of *Nephelea cuspidata* between Colombia and French Guiana may be genuine inasmuch as the intervening areas of Venezuela, British Guiana, and Surinam have provided a number of other tree fern collections without yielding this species. Most of these collections, however, are from the more coastal regions of these countries. Because it is a lowland and gallery forest species and does occur on the eastern side of the Andes, its presence in Amazonas, Brazil, near the Colombian and Peruvian borders suggests that it may yet be found in the little collected southern reaches of Venezuela, British Guiana, and Surinam and in northern Brazil along the eastern and northern edges of the Amazon basin. If it does inhabit such an arc, its range may connect to Leprieur's collection sites via the Oyapok River.

Nephelea cuspidata is known from Nicaragua, Costa Rica, Panama, Colombia, French Guiana, Ecuador, Amazonas Brazil, Peru, Bolivia, and Paraguay. It commonly occurs along river banks, in ravines, and in more or less dense wet rain forest or cloud forest from sea level to 1200 m. It is replaced at higher altitudes by other species, such as *N. erinacea*.

ADDITIONAL SPECIMENS EXAMINED: **Nicaragua. Río San Juan:** *Bunting & Licht 890* (GH); 1893, *Shimek* (F,MO); 1893, *Shimek & Smith* (MO); *C. L. Smith 2033* (GH, MO,NY,US). **Costa Rica.** 1901–1905, *Wercklé* (US); 1902, *Pittier* (NY). **Guanacaste:** *White & Lucansky 196868* (DUKE,GH). **Alajuela:** *Brade 628* (NY,US); *Nisman 71, 74* (GH). **Heredia:** *Burger & Stolze 5897* (GH); *Nisman 51, 179* (GH); *Scamman 7439* (GH); *Scamman & Holdridge 7857* (GH,US). **Limon:** *Nisman 134* (GH); *Scamman 7003* (GH,US), *7010* (GH,UC,US); *J. D. Smith 5074* (GH,US). **San José:** *Brade 94* (NY). **Panama. Canal Zone:** *Killip 2921* (US); *Shattuck 1145* (F); *Wetmore & Woodworth 116* (GH). **Darien:** *Schott 34* (F,MO,US); *Stern et al. 434* (GH.MO,UC, US). **Colombia. Norte de Santander:** *Cuatrecasas 12978B* (F,US). **Antioquia:** *Haught 2001* (GH,NY,UC,US), *4617* (NY,US). **Choco:** *Taylor 1242* (US). **Cundinamarca:** *Lindig 195* (GH). **Meta:** *Cautrecasas 4628* (F,US), *Philipson & Idrobo 1801* (US); *Schultes 922* (A,GH,US). **Valle:** *Cuatrecasas 13754, 15110* (F,GH.US), *14388, 16157* (F,GH,NY,US), *14843, 15222, 16664, 17073, 17662* (F,US). **Nariño:** *Schultes & Cabrera 19105* (GH,NY,US). **Caqueta:** *Woronow & Juzepczuk 6419* (US). **Amazonas:** *Schultes 6966* (GH). **Brazil. Amazonas:** *Duarte 6904* (HB). **French Guiana.** *Leprieur 137* (NY), *190* (F,GH,US), 1830, *Leprieur 197* (GH), 1847, *Leprieur 197* (F,US). 1847, *Leprieur 197/267* (F), *Leprieur 224* (US), *267* (F,NY), 1847, *Leprieur 267* (NY). **Ecuador. Esmeraldas:** *Sparre 18192* (GH). **Imbabura:** *Solís 12784* (F). **Napo-Pastaza:** *Grubb et al. 1551* (NY,US). **Cotopaxi:** *Sparre 17196* (GH). **Los Ríos:** *Sparre 17900* (GH). **Peru.** 1829, *Poeppig* (M). **Loreto:** *Mexia 6197* (F,GH,MO,NY,UC,US); *Ll. Williams 3288* (F,GH,NY,US). **San Martín:** *Allard 20618* (GH); *Ferreyra 4376a* (USM). **Junín:** *Killip & Smith 23986* (F,NY,US). **Cuzco:** *Vargas 11703, 14591, 15572, 16117* (GH). **Ayacucho:** *Killip & Smith 22654* (GH,US). **Puno:** *Vargas 16132, 18862, 18919* (GH). **Bolivia. La Paz:** *Buchtien 1801* (US), *3602* (F,US); *Cárdenas 805* (GH.US); *Krukoff 10079* (F,GH,MO,NY,US), *10841* (F,GH,MO,NY,UC.US); *R. S. Williams 1335* (GH,US). **Cochabamba:** *Buchtien 2195* (F,GH,US); *Cárdenas 2031* (GH,US). **Santa Cruz:** *Steinbach 16416* (GH). **Paraguay. La Cordillera:** *Balansa 2861* (P pro parte).

15. Nephelea Sternbergii

(Sternb.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

Stem to 15 m. tall and 18 cm. in diameter (including the investing sheath of adventitious roots), bearing tan to brown scales especially toward the apex and blackish spines to 11 mm. long, adventitious buds reported. *Unexpanded croziers* with blackish spines to 10 mm. long and mostly light tan scales with a dark apical seta to 1.0 mm. long, often with an additional smaller apical seta but without lateral setae. *Petiole* to ca. 0.5 m. long, brown with blackish spines to 11 mm. long, the scales on the abaxial surface copious, tan, with or without a darker central stripe, with a dark apical seta to 1.0–1.5 mm. long and with or without additional smaller apical and lateral setae. *Lamina* papyraceous to ca. 3.0–3.5 m. long and 1.4 m. wide, (rarely partially tripinnate) predominately bipinnate-pinnatifid, abruptly reduced to a distinct pinna-like apex (to ca. 30 cm. long). *Rachis* brown, adaxially furfuraceous-pubescent to glabrescent, abaxially furfuraceous-squamose, scabrous where the larger scales have fallen, to frequently glabrescent. *Central pinnae* sessile to short (to ca. 1.5 cm.) petiolulate, ovate-lanceolate, to ca. 75 cm. long and 23 cm. wide; *basal pinnae* not highly reduced, to ca. 23–32 cm. long; *pinna-rachis* adaxially pubescent, abaxially furfuraceous-squamose or, when glabrescent, with scabrous to spinose projections where the larger scales have fallen, not conspicuously pubescent distally, with mostly inconspicuous lateral pneumatodes at costa axils, narrowly greenish-alate (to ca. 0.4 mm. wide on each side) between the more distal sessile pinnules. *Pinnules* to 12.5 cm. long and 2.5 cm. wide, deeply pinnatifid (the basal segments usually free on the basiscopic side, the acroscopic side nearly always adnate; basal segments only infrequently truly sessile or free, very rarely lobate), sessile to short (to ca. 2 mm.) petiolulate, narrowly ovate to narrowly elliptic, the apex acute to frequently acuminate; *costa* adaxially pubescent, abaxially furfuraceous-squamose, sparsely pubescent distally, the scales to ca. 2 mm. long, tan, usually without a darkened central stripe and with several dark apical and lateral setae, often clustered in the axil. *Segments* sub-falcate to falcate with lateral margins entire to subentire, apex entire to crenulate, margins slightly or not revolute; *costule* adaxially frequently with one to few stiff trichomes distally, abaxially with dark-setate squamules similar to those of the costa but smaller, often with whitish highly trichomoid squamules, occasionally with sparse stiff trichomes distally; *veins* once-forked (rarely more) at or near the costule or simple, evident on both surfaces, adaxially glabrous or with occasional, minute, highly trichomoid stellate squamules especially near the segment margins, abaxially frequently with a diminishing continuation of the often substellate indument of the costule and with conspicuous to inconspicuous stellate trichomes or highly trichomoid stellate squamules to ca. 0.2–0.6 mm. in diameter; *lamina surface* adaxially and abaxially glabrous between the veins, except occasionally with highly trichomoid squamules at or near the margins. *Sori* at the forking of the veins or near the costule on simple veins; *indusium* diaphanous to tan or brown, of delicate to firm texture, cyathiform or urceolate to sphaeropteroid, intact to rupturing irregularly at maturity and persistent to more or less fugacious, with conspicuous whitish stellate indument similar to that on the veins to glabrescent; *receptacle* globose, inserted to slightly exserted, with short (to ca. 0.1–0.2 mm. long) mostly inconspicuous paraphyses.

The close relationship of this species to *Nephelea cuspidata* is especially evident because of its indument of stellate trichomes or trichomoid squamules found abaxially on the veins. It is distinct from *N. cuspidata* in detailed aspects of this same indument in the nature of its indusia, and in its more variable petiole scales. Specimens which are most like *N. cuspidata* in the color, texture, and persistence of the indusium are least like that species in their highly conspicuous whitish vein and indusial indument (Fig. 84) and in their petiole scales which generally feature a single dark seta. Those most like *N. cuspidata* in their stellate trichomoid indu-

ment and the condition of the setae on the petiole scales feature delicate and mostly fugacious indusia. Both species reach eastern Paraguay, but this is not the center of a cline between the two species. While those specimens of *N. Sternbergii* with indusial color and texture most like that of *N. cuspidata* occur more to the west in Brazil, they are found in var. *Sternbergii* which has the arms of the vein indument tending to be more numerous and irregularly disposed than in *N. cuspidata* and the petiole scales have a single apical seta and none laterally. The presence of several apical and lateral setae characterizes the petiole scales of *N. cuspidata* even in Paraguay.

KEY TO VARIETIES

Petiole base abaxially bearing light tan scales which usually lack a darkened central stripe, dark lateral setae, and more than one dark apical seta; costule abaxially with conspicuous whitish highly trichomoid stellate squamules in addition to the dark-setate squamules; abaxially the veins with stellate trichomes or highly trichomoid stellate squamules to ca. 0.5–0.6 mm. in diameter with long whitish irregular arms (Fig. 84), often especially evident near the segment margins; indusium brown, more or less firm, cyathiform to urceolate, occasionally sub-sphaeropteroid, intact to more or less rupturing at maturity, persistent, with conspicuous whitish stellate indument similar to that on the veins. Brazil, Paraguay. . . . . 15a. var. *Sternbergii.*

Petiole base abaxially bearing tan scales which often have a darkened central stripe, dark lateral setae, and more than one dark apical seta; costule abaxially usually without conspicuous whitish trichomoid stellate squamules in addition to the dark-setate squamules; abaxially the veins frequently with a diminishing continuation of the often sub-stellate dark-setate indument of the costule and with sparse, more or less inconspicuous stellate trichomes or highly trichomoid squamules to ca. 0.2–0.3 mm. diameter; indusium diaphanous to tan or light brown, delicate, sphaeropteroid to sub-sphaeropteroid rupturing irregularly at maturity and persistent to usually more or less fugacious, glabrescent to obscurely stellate pubescent. Brazil. . . . . 15 b. var. *acanthomelas.*

15a. **Nephelea Sternbergii** var. **Sternbergii**

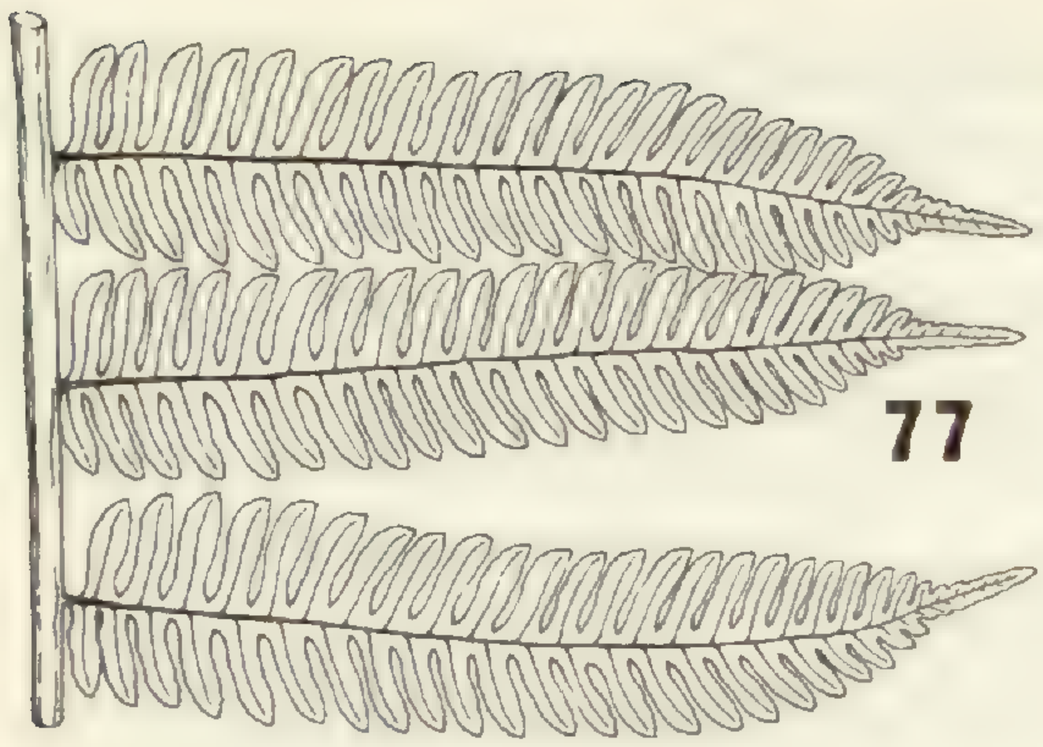
Figs. 81–84. Map 20

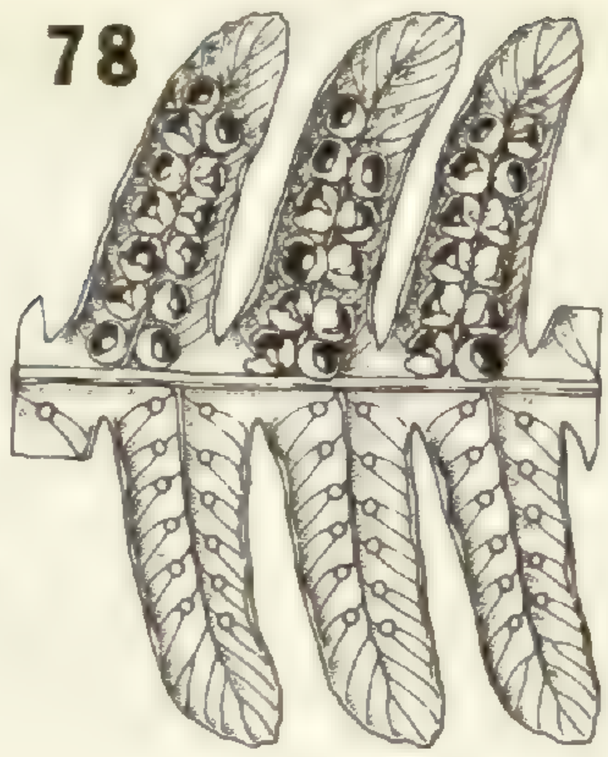
Cyathea Sternbergii Pohl ex Sternb. Fl. der Vorwelt 1:47, t.C. 1820. (Essai sur la Fl. du Monde Prim. 4:52, t. C. 1826.) TYPE: habitat in Brasiliae Capitania Goyaz ad Limoero non procul St. Izidro, *Pohl,* PRC! or perhaps W; isotypes: BR (two sheets, not seen), BM! fragment and photos of specimens at BR. PRC!. Not *Cyathea Sternbergii* Domin, Pterid, 263. 1929, nom. nov. for *Alsophila elegans* Mart., not *Cyathea elegans* Hew.

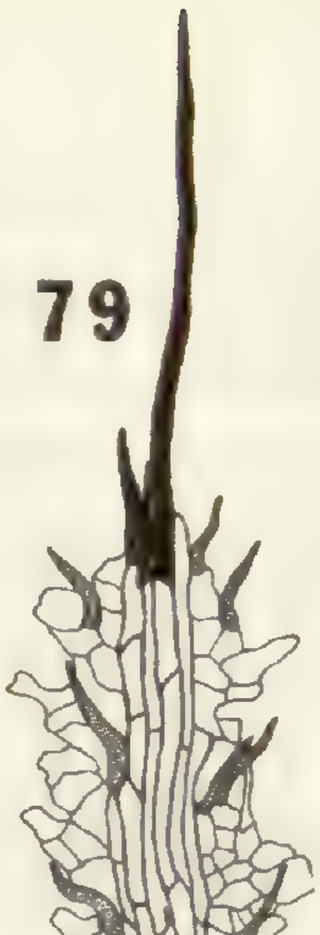
Cyathea Caesariana Christ, in Wettstein, Denkschr. Akad. Wien 79:18, t. 2, f. 2, t. 8, f. 5–6. (1908); as a separate, p. 12. (1906) 1907, fide Hieron. in Beiblatt zur Hedwigia 46(3):116–117. 1907. LECTOTYPE: Brazil, São Paulo: in circuitu urbis Cerqueiro Cesar, ca. 500 m.s.m., VII, 1901, *Wettstein & Schiffner,* P! (not herb. Christ, therefore perhaps only an isotype); syntypes (not seen): In sylvaticis inter Apiahy et Yporanga, 900–400 m., VIII 1901, *Wettstein et Schiffner;* Ad ripas fluminis Rio Branco Prope Conceição de Itahaen, 20–100 m., VII 1909, *Wettstein et Schiffner.*

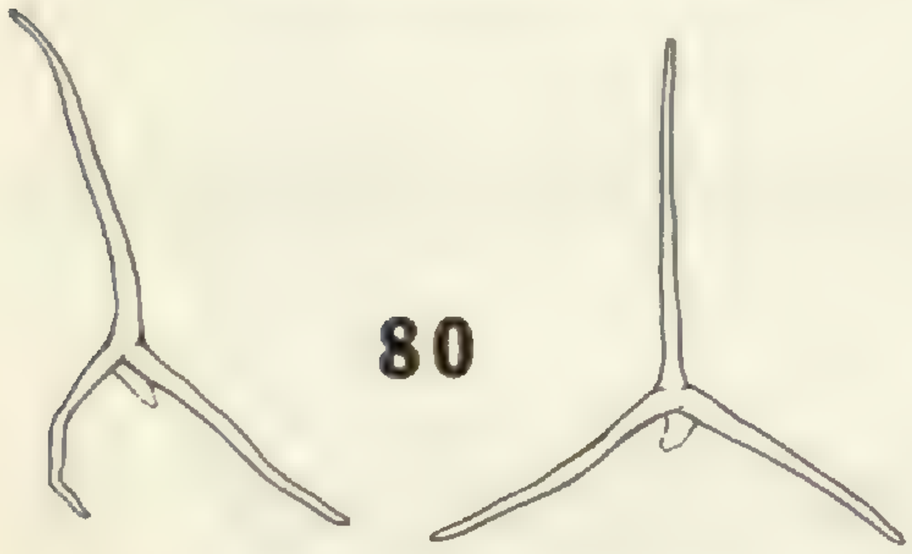
Hemitelia Caesariana (Christ) Samp. Bol. Mus. Nac. Rio Janeiro 1:19. 1923.

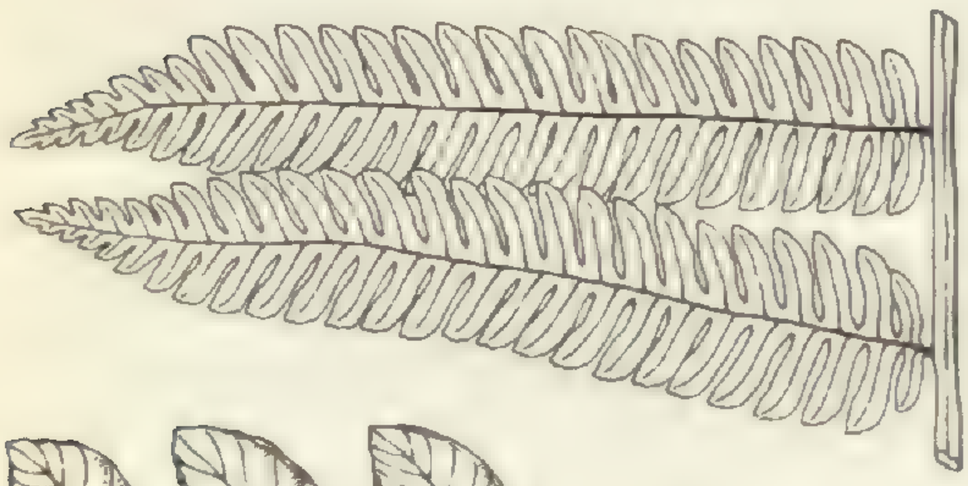
Cyathea Rojasii Christ, Fedde Repert. 6:348. 1901. LECTOTYPE: Paraguay, Amambay: Sierra de Amambay, ad ripas rivulorum pr. Punta Porá, *Hassler 10414* (leg. *Rojas*), P! (three sheets, one herb. Christ, one herb. Bonaparte, one herb. Christ and herb. Bonaparte; although only two sheets bear Christ's herbarium labels, the third should also be included in the holotype because it includes the petiole as described in the protologue). SYNTYPE: *Hassler 10021* (leg. *Rojas*), not found at P by Rolla Tryon in 1969; isosyntype NY!.

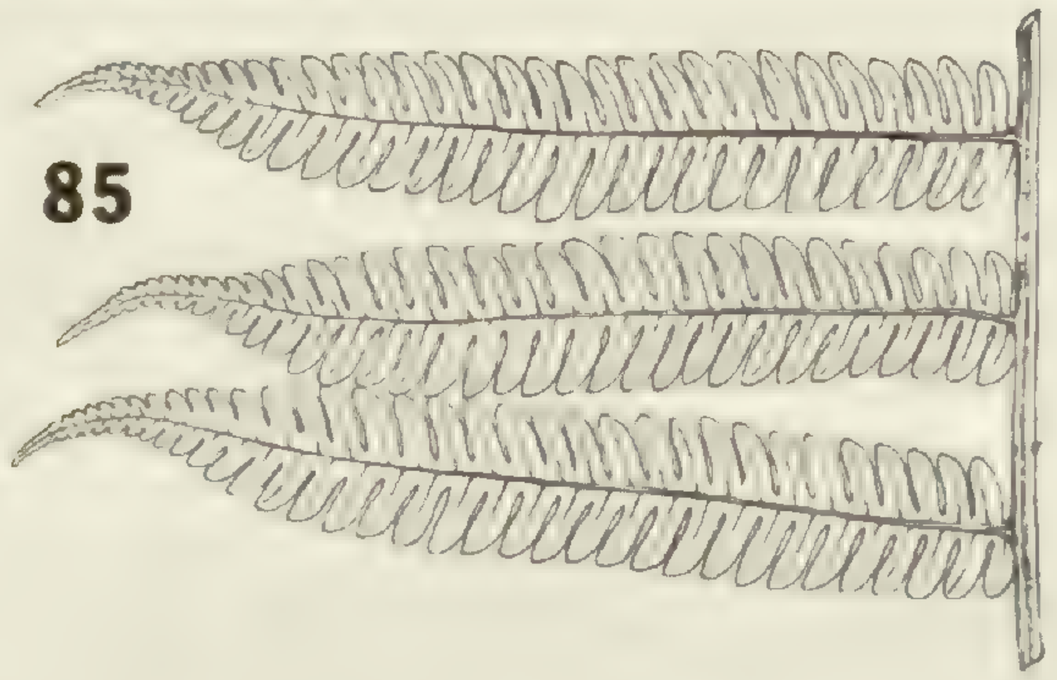












FIGS. 77–80. Nephelea cuspidata: 77, Central pinnules of a central pinna, *Asplund 16330* (S), × 0.5; 78, Central portion of a pinnule in 77, × 2; 79, Distal portion of a scale from the abaxial petiole surface, structurally marginate with a prominent dark apical seta and several additional smaller dark apical and lateral setae, *Cuatrecasas 17073* (US), × 43; 80, Representative stellate trichomes from the abaxial vein surface, with three distinct rigid arms, *Scamman & Holdridge 7857* (GH), × 85. FIGS. 81–84. Nephelea Sternbergii var. Sternbergii: 81, Central pinnules of a central pinna, *Regnell 2479* (MO), × 0.5; 82, Central portion of a pinnule in 81, with cyathiform indusia, × 2; 83, Central portion of a pinnule as shown in 81, with sub-sphaeropteroid indusia, *Mexia 4650* (GH), × 2; 84, A representative highly-trichomoid stellate squamule from the abaxial vein surface, with long irregular arms, *Burchell 5339* (GH), × 85. FIGS. 85–87. Nephelea Sternbergii var. acanthomelas: 85, Central pinnules of a central pinna, *Dusén 10346* (F), × 0.5; 86, Central portion of a pinnule in 85, with unruptured sphaeropteroid indusia, ×2; 87, Central portion of a pinnule as shown in 85, but more fertile, *Brade 42967* (F), × 2.

Cyathea schizolepis Copel. Univ. Calif. Publ. Bot. 17:27, t. 3. 1932. TYPE: Brazil, Minas Gerais, Viçosa, Fazenda de Aguada, in dense forest, alt. 725 m., *Mexia 5059*, UC 466087–466090!; isotypes: F!, GH! (two sheets), MO! NY!, US! (three sheets).

Stem diameter not known, bearing mostly light tan scales especially toward the apex and blackish spines to 11 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 10 mm. long and mostly light tan scales with a dark apical seta to 1.0 mm. long, often with an additional smaller apical seta but without lateral setae. *Petiole* with scales on the abaxial surface tan, usually without a darkened central stripe, with a dark apical seta to 1.0–1.5 mm. long and usually without additional apical and lateral setae. *Lamina* bipinnate-pinnatifid. *Basal pinnae* not highly reduced, to ca. 32 cm. long. *Pinnules* with the basal segments usually free on the basiscopic side, the acroscopic side nearly always adnate. *Costule* abaxially with dark-setate squamules similar to those of the costa but usually smaller and with whitish highly trichomoid stellate squamules, occasionally with sparse stiff trichomes distally; *veins* adaxially glabrous or with occasional minute highly trichomoid stellate squamules especially near the segment margins, abaxially with stellate trichomes or highly trichomoid stellate squamules to ca. 0.5–0.6 mm. in diameter with long whitish irregular arms, often especially evident near the segment margins. *Indusium* brown, of more or less firm texture, usually cyathiform to urceolate, occasionally sub-sphaeropteroid, intact to more or less rupturing at maturity, persistent, bearing conspicuous whitish stellate indument similar to that on the veins.

Dr. Riedl at the Naturhistorisches Museum, Vienna, has informed me that the type of *Cyathea Sternbergii* cannot now be found there among Pohl's specimens. Likewise, Dr. Soják at the Botanical Department of the National Museum in Prague, which holds the Sternberg Herbarium, indicated that the type material is not there. Dr. Soják referred me to the herbarium of Charles University in Prague where a Pohl collection was found.

This variety generally occurs more inland than variety *acanthomelas*. In their most characteristic condition, the petiole scales of variety *Sternbergii* have a single dark seta and are more or less golden tan (due to lack of a darkened central stripe) and the indusia are brown, firm, persistent, and conspicuously stellate pubescent.

Variety *Sternbergii* occurs in Brazil in the states of Minas Gerais, São Paulo, and Goias and in Paraguay in the Departments of Amambay (Sierra de Amambay) and La Cordillera at altitudes of ca. 500–690 m. in forest and along rivers in gallery forest.

ADDITIONAL SPECIMENS EXAMINED: **Brazil.** *Clausen 257* (US). **Goias:** *Dawson 14968* (US); *Ule 526* (R). **Minas Gerais:** *Mexia 4650* (F,GH,MO,NY,R,UC,US); *Mosén 2037* (S), *2038* (R.S); *Santos & Castellanos 24124* (HB). **São Paulo:** *Burchell 5339* (GH); 1913, *Edwalle* (SP); *Regnell 1479* (F,MO,US). **Paraguay. La Cordillera:** *Balansa 2861* (F,P pro parte).

15b. **Nephelea Sternbergii** var. **acanthomelas** (Fée) Gastony, comb. et stat. nov.

FIGS. 85–87, MAP 21

Cyathea acanthomelas Fée, Crypt. Vasc. Brésil **1**:177, t. 64, f. 1. 1869. TYPE: in Brasilia fluminensi, *Glaziou 379*, P!; isotype P! in herb. Glaziou; isotype portion: US! ex herb. Rosenst.

Nephelea Sternbergii forma *acanthomelas* (Fée) Brade, Bradea 1 (10): 74. 1971.

Cyathea Sampaioana Brade et Rosenst. Bol. Mus. Nac. Rio 7:137, t. 1, 4. 1931. TYPE: habitat in Brasilia statu Rio de Janeiro, prope Teresopolim (Corrego Beija-Flor), 1200 m., 7 X 1929, *A. C. Brade 9601* (erroneously cited in the protologue as *9631*), Herb. Mus. Nac. no. 20616, R! consisting of six sheets; isotypes B!, NY!, UC!.

Nephelea Sternbergii forma *Sampaioana* (Brade et Rosenst.) Brade, Bradea 1 (10): 74. 1971.

Stem to 18 cm. diameter, bearing tan to brown scales especially toward the apex and blackish spines (length not known), adventitious buds reported on one specimen. *Unexpanded croziers* not known. *Petiole* with scales on the abaxial surface tan, often with a darkened central stripe, with a dark apical seta to 1 mm. long and often with additional smaller apical and lateral setae. *Lamina* (rarely partially tripinnate) predominantly bipinnate-pinnatifid. *Basal pinnae* not highly reduced, to ca. 23 cm. long. *Pinnules* with the basal segments usually free on the basiscopic side, the acroscopic side adnate, only infrequently truly sessile or free, very rarely lobate. *Costule* abaxially with dark-setate squamules similar to those of the costa but usually smaller, occasionally with sparse stiff trichomes distally; *veins* adaxially glabrous, abaxially frequently with a diminishing continuation of the often sub-stellate and dark-setate indument of the costule and with sparse, more or less inconspicuous, stellate trichomes or highly trichomoid squamules (to ca. 0.2–0.3 mm. diameter). *Indusium* diaphanous to tan or light brown, of delicate texture, sphaeropteroid to sub-sphaeropteroid, rupturing irregularly at maturity and persistent to usually more or less fugacious, glabrescent to obscurely stellate pubescent.

This variety is usually more coastal than var. *Sternbergii*. In their most characteristic condition the scales borne abaxially on the petiole base have several dark apical and lateral setae and the indusia are diaphanous to tan, delicate, fugacious or partially so, and glabrescent or only obscurely stellate pubescent. Minute dark-setate squamules are generally more common abaxially on the costule and veins in this variety than in var. *Sternbergii* and the trichomoid squamules on the veins are less conspicuous. The minute one- or two-celled trichomules which are commonly (but usually obscurely) present on the abaxial surface of fern leaves are certainly present in both varieties of this species but are frequently more conspicuous (with a tan to claret cast) abaxially on the veins of var. *acanthomelas*.

The scabrous abaxial surface of the pinna-rachis is occasionally more pronounced in var. *acanthomelas* than in the preceding one. This is especially shown in some specimens from Paraná (e.g., *Dusén 10346*) where these scabrous projections may be seen as small squaminate spines.

Brade (1971) has recently concluded that *Cyathea acanthomelas* and *C. Sampaioana* are distinct only at the rank of *forma*. I am unable to assign even that degree of taxonomic recognition to them. In the same paper, Brade pointed out what appeared to be vegetative reproduction by stolons in a specimen of *C. Sampaioana* and discussed the presence of adventitious buds at the base of the stem in one individual. Although adventitious buds are known in other species of *Nephelea*, reproduction by stolons does not appear to have been reported elsewhere in the genus. The phenomenon reported by Brade may be similar to the stolon reproduction described by Halle (1966) in *Alsophila Manniana* (Hook.) Tryon (as *Cyathea Manniana* Hook.) in Africa.

Variety *acanthomelas* occurs in Brazil in the states of Bahia, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina at altitudes of ca. 50–1200 m. along rivers and in rain forests, especially along the Serra do Mar.

ADDITIONAL SPECIMENS EXAMINED: **Brazil.** *Glaziou 2379* (NY); *Luederwaldt SP 22027* (SP). **Bahia:** *Blanchet*, herb. Luerssen 6145 (UC), *Blanchet 2489* (MO,NY,US), *2506* (F,K,NY); *Pohl 193* (P). **Rio de Janeiro:** *Brade 16582* (GH,MO,NY,S,US), *16642* (F, GH,MO,NY,R,S,US); *Burchell 2545* (GH); *1872, Glaziou* (MO), *R 8725* (R); *Lima 11, 17, 26* (R); *Pabst et al. 7377* (HB); *Schwacke R8726* (R). **São Paulo:** 1928, *Brade* (NY,R,UC), *6902* (NY), *8221* (R,US), *R15743* (R); *Luederwaldt 6635* (SP); *Mosen 3096* (P,R,S). **Paraná:** *Dusén 724a* (GH,MO), *6734* (F,GH,MO), *6775* (F,GH,MO,NY,S,US), *10112* (GH,S), *10346* (GH,MO,NY,S,UC,US), *12037* (GH); *Hatschbach 11283* (HB). **Santa Catarina:** *Schmaltz 47* (F,MO,NY,P,S,UC).

16. **Nephelea incana** (Karst.) Gastony, comb. nov.

FIGS. 88–90, MAP 22

Cyathea incana Karst. Fl. Columbiae 1:75, t. 37. 1860. TYPE: Columbia, Cundinamarca: crescit in silvis frondosis andium Bogotensium, altitud. 2500 m., *Lindig;* authentic material (Villeta, 1900 m.) LE! and P!, a sheet at B! and one at W (BM! photo and fragment ex W) are probably the same as these, but are labeled "leg. *Karsten.*"

Cyathea sprucei Hook. Syn. Fil. 20. 1865. LECTOTYPE: Ecuador, Montaña de Canelos, alt. 4500 ft., Tungurahua, alt. 6500 ft., Maio 1858, *Spruce 5428* K! a collection consisting of two sheets; isotypes: NY! two sheets and fragment ex K, P!. *Spruce 5744* P! is rejected as a type; it is *Nephelea mexicana* (Schlect. & Cham.) Tryon, (K sheet not seen).

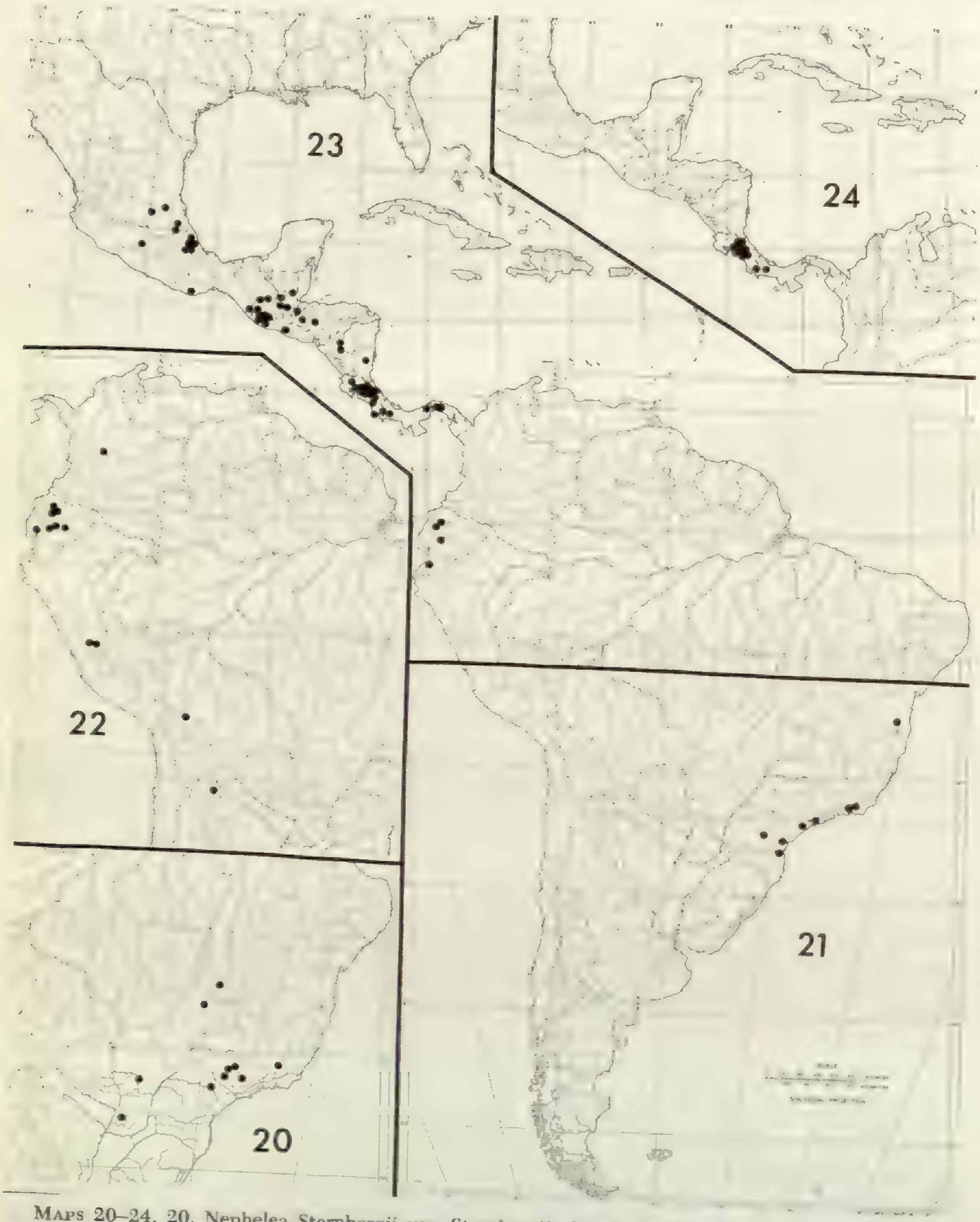
Cyathea canescens Sod. Sert. Fl. Ecuad. II, 4. 1908. "Ecuador, Pichincha: cresit in silvis suband. et subtrop. vulc. Pichincha et Atacatzo." LECTOTYPE: 7/907 *Sodiro* in silv. suband. vulc. Atacatzo (ut *C. incanae* Karst. affinis, tamen diversa videtur) P!; isolectotypes: MO!, UC!, US!. The protologue is obviously based on more complete material, but this fits the description and reflects Sodiro's remarks in the protologue as to its affinity with *C. incana* Karst. Syntype: vulc. Pinchincha, *Sodiro* P! (two sheets).

Nephelea canescens (Sod.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

Cyathea O'Donelliana Alston, Lilloa 30:108, t. 1–2. 1960. LECTOTYPE: Argentina, Salta: Orán, St. Andrés, 1000 m., *Willink 285* BM!; isolectotype: A!. SYNTYPE: 24 May 1949, *O'Donell,* from Orán, cultivated at Instituto M. Lillo, BM!.

Stem to 4.5 m. tall, diameter not known, bearing tan to light brown scales especially toward the apex and blackish spines to 8 mm. long, adventitious buds not known. *Unexpanded croziers* with blackish spines to 8 mm. long and light tan scales with a usually solitary dark apical seta to 1–1.5 mm. long (rarely longer) and without lateral setae. *Petiole* to 0.15–0.35 m. long (to the highly reduced basal pinnae), light brown to brown with blackish spines to 4 mm. long, the scales on the abaxial surface copious, mostly light tan, some with a darker central stripe, with a dark apical seta to 1–2 mm. long and without lateral setae (or an additional apical or lateral seta only rarely). *Lamina* rigidly papyraceous, length not known, to ca. 1 m. wide, bipinnate-pinnatifid, abruptly reduced to a distinct pinna-like apex (to ca. 20 cm. long). *Rachis* light brown, adaxially furfuraceous-pubescent, abaxially furfuraceous-glabrescent. *Central pinnae* short (to ca. 1 cm.) petiolulate, narrowly elliptic-lanceolate to narrowly ovate-lanceolate, to ca. 60 cm. long and 16 (usually less) cm. wide; *basal pinnae* often highly reduced to ca. 7 cm. long; *pinna-rachis* adaxially pubescent, abaxially furfuraceous-glabrescent to pubescent with crispate trichomes, with lateral pneumatodes at costa axils not evident, narrowly (ca. 0.25–0.5 mm. wide on each side) greenish-alate between the more distal sessile pinnules. *Pinnules* to ca. 9 cm. long and 1.8 cm. wide, more or less deeply pinnatifid (the basal segments usually free on the basiscopic side, the acroscopic side adnate), sessile to short (to ca. 1 mm.) petiolulate,

narrowly ovate to narrowly triangular, the apex acute to acuminate; *costa* adaxially pubescent, abaxially pubescent and with occasional small, tan, dark-setate scales, the scales not significantly clustered in the axil. *Segments* straight to sub-falcate with lateral margins and apex subentire to serrate-dentate, margins more or less revolute; *costule* adaxially glabrous, occasionally with a stiff trichome distally, abaxially pubescent to squamulose with highly trichomoid (rarely dark-setate) squamules; *veins* commonly simple but often once-forked at or near the costule, evident on both surfaces, adaxially glabrous, abaxially glabrous or with occasional crispate trichomes; *lamina surface* adaxially and abaxially glabrous between the veins, except occasionally with more or less crispate, simple or branched trichomes at or near the margins. *Sori* at or near the costule on simple veins or at the forking of the veins; *indusium* meniscoid to shallowly



Maps 20–24. 20, Nephelea Sternbergii var. Sternbergii; 21, N. Sternbergii var. acanthomelas; 22, N. incana; 23, N. mexicana; 24, N. polystichoides.

or deeply cyathiform or sub-sphaeropteroid, diaphanous to light brown, of more or less delicate texture, persistent with those more sphaeropteroid often lobed or ruptured at maturity, pubescent with more or less soft and often crispate trichomes or trichomoid processes, these occasionally biseriate to multiseriate at their bases; *receptacle* columnar to globose, usually slightly exserted with short (to ca. 0.1–0.25 mm. long) paraphyses, inconspicuous to notably tufted at the apex of the receptacle.

In addition to the characters in the key, the long, narrow, often almost filiform, light tan scales on the petiole base serve to characterize this species. The scales borne abaxially on the petiole base have a dark apical seta often up to 2 mm. long, the longest in the genus. I have seen only one petiole base from Argentina and that is from the syntype of *Cyathea O'Donelliana* cultivated at the Instituto M. Lillo. In view of the congruence of all other critical characters in the Argentine material, the lack of the characteristic long tan scales from this petiole is taken to be an aberrancy of the individual, perhaps related to the conditions of its cultivation.

As in *Nephelea Grevilleana* and *N. crassa* and occasionally elsewhere, the morphology of many of the paraphyses is suggestive of sporangial derivation, especially when the paraphyses are more or less tufted at the apex of the receptacle. The pinnules occasionally disarticulate from the pinna-rachis in this species as in several others in the genus.

The distribution of *Nephelea incana* based on the few presently available specimens is quite discontinuous, reflecting the need for more collections from the Andes. *Nephelea incana* is known from Colombia, Ecuador, Peru, Bolivia, and northern Argentina in wet forest on mountain slopes, in ravines, and along rivers and road banks at altitudes of ca. 800–2500 m.

ADDITIONAL SPECIMENS EXAMINED: **Ecuador. Pichincha:** 1907, *Mille* (US); 1907, *Sodiro* (NY), *US 2427083* (A,US). **Tungurahua:** *Bell 809* (GH,S). **Guayas:** *André 3656* (NY). **Peru. Junín:** *Esposto 670* (USM); *Iltis & Iltis 249* (GH). **Bolivia. La Paz:** *Herzog 1605* (UC). **Argentina. Salta:** *Capurro 245, 279, 292* (LIL); *Nervoorst 440* (LIL).

17. Nephelea mexicana

(Schlect. & Cham.) Tryon, Contrib. Gray Herb. 200: 40. 1970.

FIGS. 91–94, MAP 23

7302 *Cyathea mexicana* Schlet. & Cham. Linnaea **5**:616. 1830. TYPE: Mexico, Jalapa, *Schiede*, B (seen and confirmed by Rolla Tryon in 1969); isotype: BM!, a fragment of *Schiede 802* NY! ex B is doubtless authentic; photo UC! of isotype in herb. J. Sm. at K.

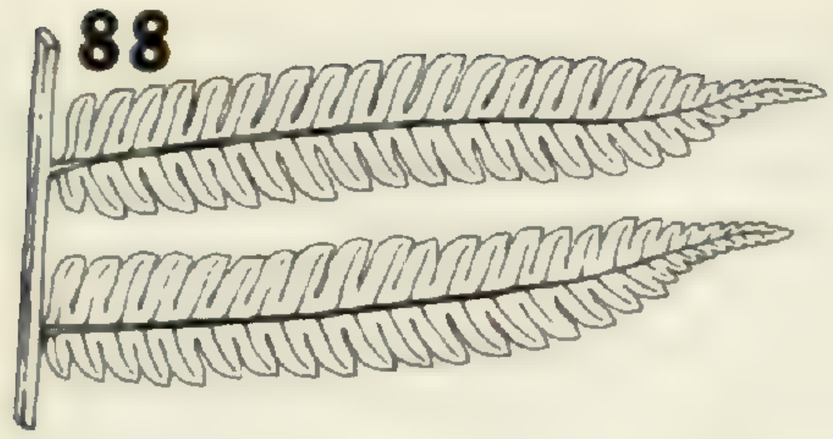
Cyathea articulata Fée, Mém. Fam. Foug. **8**:111. 1857. TYPE: Mexico, Villa-Alta et Talea, *Galeotti 6531*, probably BR; istotypes: B (not seen), NY! fragment ex B, P! in herb. Fournier.

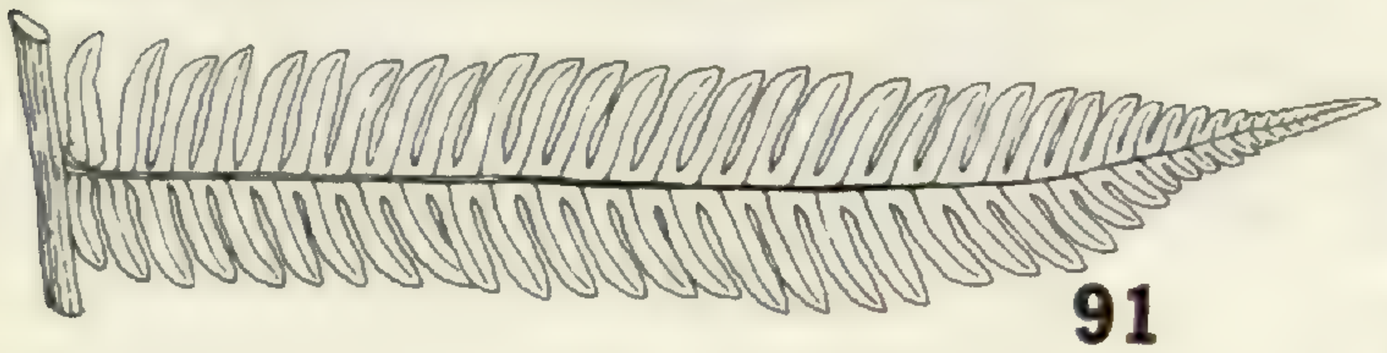
Hemitelia firma Baker, Jour. Bot. **15**:161. 1877. TYPE: Ecuador, collected in the Andes of Quito, August, 1875, *Sodiro* K!; isotypes: P! (two sheets), US! fragment ex Rosenstock.

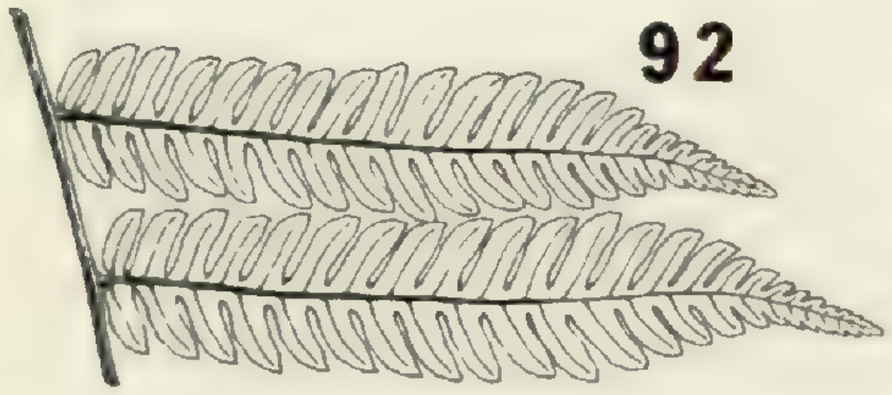
Cyathea firma (Baker) Domin, Pterid. 264. 1929, not Mett. ex Kuhn, 1869.

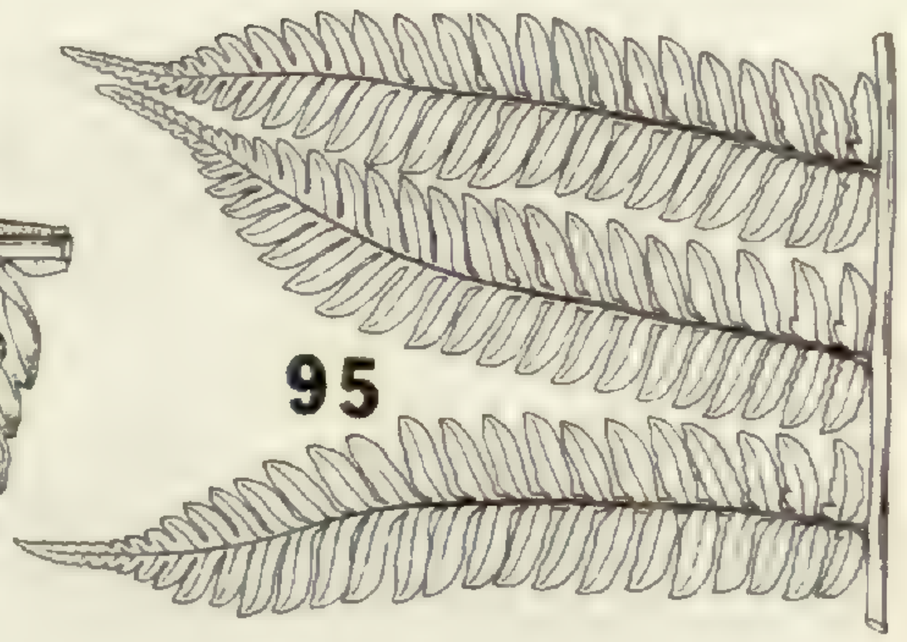
Cyathea firmula Domin, Acta Bot. Bohm. **9**:115. 1930, nom. nov. for *Hemitelia firma* Baker, not *Cyathea firma* Mett. ex Kuhn.

Cyathea patellaris Christ, Ann. Conserv. Jard. Bot. Geneve **4**:207. 1900. TYPE: Costa Rica, bords du Río de Las Vueltas, Tucurrique, alt. 631 m., Nov. 1898, *Tonduz*









FIGS. 88–90. Nephelea incana: 88, Central pinnules of a central pinna, *Lindig 183* (P), × 0.5; 89, Central pinnules of a central pinna, July 1907, *Sodiro* (MO), × 0.5; 90, Central portion of a pinnule as shown in 89, with shallowly cyathiform indusia, *Bell 809* (GH), × 2. FIGS. 91–94. Nephelea mexicana: 91, Central pinnule of a central pinna, *Pittier 3904* (US), × 0.5; 92, Central pinnules of a central pinna, *Pringle 7892* (GH), × 0.5; 93, Central portion of a pinnule in 92, with unruptured sphaeropteroid indusia, ×2; 94, Adaxial view of distal pinna-rachis showing the alate condition between the more distal sessile pinnules as well as between the adnate pinnules, *Gastony & Gastony 784* (GH), × 2. FIGS. 95–98: Nephelea polystichoides, all alate between tertiary segments; 95, Central pinnules of a central pinna, *Nisman 111* (GH), × 0.5; 96, Central pinnule of a central pinna, more complex than those in 95, 1903, *Wercklé* (P), × 0.5; 97, Central pinnule of a central pinna, representative of the most complex leaf form in the species and the genus, *Nisman 49* (GH), × 0.5; 98, Central portion of a pinnule as shown in 95–97 but of intermediate complexity, with unruptured sphaeropteroid indusia, 1904, *Wercklé*, Herb. Nac. Costa Rica no. 16787 (P), × 2.

12783, no specimen found by Rolla Tryon in 1969 in Christ's herbarium at P; isotypes: F! fragment in herb. Jeanpert, GH!, M!, NY! (two sheets, one a fragment ex Christ), P! (two sheets, one in herb. Bonapart), US! (two sheets, one a fragment).

Nephelea patellaris (Christ) Tryon, Contrib. Gray Herb. 200:40. 1970.

Alsophila costalis Christ, Bull. Herb. Boiss. II, 4:951. 1904. TYPE: Costa Rica, colectée s.i.l. par Mm. *Wercklé et Brune* probablement au voisinage de Turrialba, leur domicile, P! (probable, annotated as n. sp. herb. Christ, but does not include Brune's name as collector); isotype: NY! fragment ex Christ.

Cyathea costalis (Christ) Domin, Pterid. 262. 1929.

Alsophila furcata Christ, Bull. Herb. Boiss. II, 4:957. 1904. TYPE: Costa Rica, Turrialba, Azul-Quelle, *Wercklé et Brune,* P! (probable, annotated as n. sp. herb. Christ, but does not include Brune's name as collector).

Cyathea furcata (Christ) Domin, Pterid. 262. 1929.

Alsophila tenerifrons Christ, Bull. Herb. Boiss. II, 4:959. 1904. TYPE: Costa Rica, Jiménez, 200 m., Mrs. 1902, leg. *Alfaro* (Herb. Instit. physico-geogr. nat. Costarricensis no. 16509), specimen in herb. Christ not found at P by Rolla Tryon in 1969; isotypes: GH! pinnule ex P isotype, NY!, P! in herb. Tonduz, US! fragment from P isotype or from missing holotype.

Cyathea tenerifrons (Christ) Domin, Pterid. 263. 1929.

Nephelea tenerifrons (Christ) Tryon, Contrib. Gray Herb. 200:40. 1970.

Cyathea arida Christ, Bull. Herb. Boiss. II, 6:180. 1906. SYNTYPES: Costa Rica, Navarro Luna, 1400 m., *Wercklé 16757, 16780;* alto de Mano de Tigre, Diquis 700 m., *Pittier 12097*. None of these collections were found at P under this name by Rolla Tryon in 1969. An authentic sheet at P!, 1905, *Wercklé* at Navarro 1400 m. (does not include "Luna" as part of the locality) may be taken to fix the application of the name until the collections cited by Christ are located. Five other sheets from Christ's herbarium, 1901–1905, *Wercklé* are at NY!

Cyathea gemmifera Christ, in Jiménez, Bol. Fomento Org. Min. Fomento San José, Costa Rica 3:661, c. fig. 1913. TYPE: Costa Rica, Cerros del Tremedal, San Ramón, Abril de 1913, *Tonduz* herb. Jiménez 913 (=Herb. Nac. Costa Rica no. 17563), CR (not seen); isotypes: A!, F!, P!, UC!; isoparatypes: *Tonduz,* herb. Jiménez 915 (=Herb. Nac. Costa Rica no. 17564) F!, GH!, MO!, P! (two sheets); *Tonduz,* herb. Jiménez 914 (=Herb. Nac. Costa Rica no. 17565) F! (two sheets), UC!. Note that Figs. 1, 5, and 6 in this publication are of *Jiménez,* herb. Jiménez 909, Hacienda Violia, San Ramón, Julio 1913 and this specimen is *Nephelea polystichoides* (Christ) Tryon, F!, US!.

Stem to 10.5 m. tall and 30 cm. in diameter (including the investing sheath of adventitious roots) bearing brown scales especially toward the apex and blackish spines to 12 mm. long, occasionally with adventitious buds. *Unexpanded croziers* with blackish spines to 15 mm. long and brownish scales with a dark apical seta to 1 mm. or less long and often with smaller additional apical and lateral setae. *Petiole* to 1.2 m. long, brown to grayish-brown with blackish spines to 10 mm. long, the scales on the abaxial surface sparingly persistent, brown to tan with a darkened central stripe, with a dark apical seta to 1.5 mm. long and often with smaller additional apical and lateral setae. *Lamina* papyraceous to rigidly papyraceous or subcoriaceous, to ca. 3.2 m. long and 1.4 m. wide, (rarely partially tripinnate) predominantly bipinnate-pinnatifid, abruptly reduced to a distinct pinna-like apex (to ca. 42 cm. long). *Rachis* brown, adaxially minutely pubescent to glabrescent, abaxially furfuraceous-glabrescent. *Central pinnae* sessile to short (to ca. 2.0 cm.) petiolulate, ovate-lanceolate, to 87 cm. long and 20 cm. wide; *basal pinnae* reduced, to ca. 17–30 cm. long; *pinna-rachis* adaxially pubescent, abaxially furfuraceous-glabrescent to more or less pubescent distally, with inconspicuous to slightly swollen and conspicuous lateral pneumatodes at costa axils, narrowly greenish-alate (to ca. 0.25–0.5 mm. wide on each side) between the more distal sessile pinnules. *Pinnules* to 15 cm. (usually less) long and 2.5 cm. wide, mostly deeply pinnatifid (the basal segments often free on the basiscopic side, the acroscopic side adnate; only rarely are basal segments truly sessile or free, and even more rarely lobate), sessile to short (to ca. 2 mm.) petiolulate, narrowly ovate to narrowly obovate, the apex acute to acuminate; *costa* adaxially pubescent, abaxially furfuraceous-squamose to glabrescent, sparsely pubescent distally, the scales

to ca. 2 mm. long, tan, with several dark apical and lateral setae, infrequently clustered in the axil. *Segments* falcate to subfalcate with lateral margins and apex entire to serrate-crenate, margins more or less revolute; *costule* adaxially usually with one to several stiff trichomes distally or glabrous, abaxially glabrescent to sparsely pubescent distally, sparsely and obscurely squamose proximally, the squamules light tan, to ca. 0.5 mm. long, dark-setate or often with non-dark trichomoid processes; *veins* once (occasionally more) forked to simple (often the basal veins simple, central veins forked, distal veins simple), evident on both surfaces, adaxially glabrous, abaxially glabrous or occasionally with an obscure more or less araneose squamule; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at the forking of the veins or near the costule on simple veins; *indusium* sphaeropteroid to sub-sphaeropteroid, with or without an apical umbo, diaphanous to whitish or tan, of delicate to very delicate texture, usually fugacious at maturity or upon drying of the sorus, often only a remnant remaining around the base of the receptacle, glabrous or occasionally with one to few minute, often trichomoid squamules, these quite obscure except for an occasional dark seta; *receptacle* globose, inserted before loss of the indusium, with short (to 0.1–0.3 mm. long) mostly inconspicuous paraphyses.

Four sheets were found under the name *Cyathea arida* Christ at P! by Rolla Tryon in 1969. Two are in Christ's herbarium and were collected in Costa Rica by *Wercklé* in 1904 without specific locality, a third is without collection data or any indication that it is part of the Christ herbarium, and the fourth is in Christ's herbarium and was collected by *Wercklé* in 1905 in Navarro, Costa Rica at 1400 m. All four are annotated *C. arida* n. sp. The data associated with the fourth sheet brings it closer than any others I have seen to the syntypes cited by Christ. Although it was collected at Navarro, it is not annotated Navarro Luna. I do not wish to choose a lectotype until specimens with the full locality and numbers cited by Christ are seen.

Two factors which have contributed to the confused taxonomy and substantial synonymy associated with this taxon are the varying degrees of persistence of the indusium and the variation in details of size and shape of the leaf segments.

Because the indusia are sphaeropteroid to sub-sphaeropteroid and quite delicate, they are often nearly completely fugacious both in fully mature and nearly mature sori which have been dried in the course of making herbarium specimens. Although critical examination reveals the presence of an indusial remnant at the base of the receptacle in these specimens, such remnants were often overlooked and these specimens were described or identified in the genus *Alsophila*. Also indusial fragments were mistaken for the complete form of the indusium, for example, in the case of *Hemitelia firma*. Those specimens which retained the indusium were attributed to the genus *Cyathea*.

The size and shape of the pinnules and their associated venation patterns are also variable in this taxon. A comparative study of a large number of specimens indicates that there is a continuous series of variation from smaller to larger and more complex pinnules. This has not been previously recognized, especially in determining material from Costa Rica. Specimens with the smallest pinnules, simplest venation, and greatest uniform-

ity of ultimate segment cutting generally have been referred to *Cyathea mexicana;* those with somewhat larger pinnules, more forked venation, and some separation of sub-basal and basal segments (often with the basiscopic side of the sub-basal segments decurrent to the basal segments) to *C. patellaris;* and those with the largest pinnules, the greatest incidence of forked veins, and more coriaceous texture to *Alsophila tenerifrons.*

It is now clear that the venation pattern and the extent of lamina surface are correlated. Small pinnules or those with small ultimate segments have simple veins, whereas the larger pinnules with larger ultimate segments have forked veins (rather than a greater number of simple veins). All intermediate conditions may be observed. Also associated with the larger pinnules and larger ultimate segments is a tendency for the most basal segments to be less adnate than in the smaller pinnules.

In addition to specimens of *Nephelea mexicana* from Panama and Ecuador which fall within the central variation of the species, a few collections from these countries represent a more extreme variation characterized by larger size and greater coriaceousness of their pinnules. Because no reliable critical characters are associated with the latter conditions, these plants are not considered to be of taxonomic significance.

As in *Nephelea erinacea* and *N. polystichoides,* the leaves of *N. mexicana* have often been observed in apparent whorls of four or five (the former giving the trunk a squarish cross section). Furthermore, as in these and other species of *Nephelea,* the pinnules occasionally disarticulate from the pinna-rachis.

Nephelea mexicana occurs in Mexico, Guatamala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and Ecuador at altitudes of ca. 50–2500 m. in cloud forest or on rain forest slopes, in ravines, along streams, road banks and in more or less exposed to shaded sites of dense woods. In Guatemala it is often noted as occurring on south-facing slopes and in Mexico and Nicaragua it is frequently found in association with *Quercus* and *Liquidambar.*

ADDITIONAL SPECIMENS EXAMINED: **Mexico.** *Jurgensen 911* (NY); *Kerber 95a* (NY); *Liebold 50* (NY). **San Luis Potosí:** *Graber 272* (GH,MO,UC). **Hidalgo:** *Moore 5051* (GH,UC). **México:** *Hinton 3629* (GH). **Puebla:** *Clausen & Edwards 7471* (UC); *Fröderström & Hultén 810* (NY); *Rzedowski 23421* (US). **Vera Cruz:** *Bourgeau 1942, 2793* (NY), *2794, 2794 bis* (GH,NY); *Conzatti 801* (F); *Copeland 14* (GH,UC); *Fink 1* (NY,UC), *2* (GH,NY); *Galeotti 6335* (NY); *Gastony & Gastony 993* (GH); *Hahn 1942* (GH); *Keller 172* (F); *Müller 1855* (NY); *Pringle 6088* (F,NY), *7892* (GH); *Purpus 12* (UC), *4255* (M,UC); *C. L. Smith 2009* (GH,NY), *2184* (F.MO); *Spence 2* (GH). **Oaxaca:** *Mickel 1089* (UC), *1324* (US). **Chiapas:** *Purpus 6766* (F,GH,MO,NY,UC). **Guatemala. Huehuetenango:** *Steyermark 48880* (F,US), *51736* (F,GH.US). **San Marcos:** *Steyermark 36866* (F,GH). **Quezaltenango:** *Skutch 1410* (GH); *Standley 86662* (US); *Steyermark 33309, 33424, 33540* (F,US), *33311* (F,GH). **Suchitepequez:** *Brenckle 47–192* (F,NY); *Steyermark 46778* (F,GH,US), *46837* (US). **Peten:** *Contreras 2272* (US). **Alta Verapaz:** 1936, *Hatch & Wilson* (GH,UC); *Johnson 957* (F,GH,NY). *965* (GH); *Steyermark 45704* (F); *Türckheim 2108* (GH,M,NY). **Izabal:** *Steyermark 41930* (F,GH,US). **El Salvador. Ahuachapán:** *Standley 20199* (GH). **Honduras. Comayagua:** *Steeves & Ray 485* (GH); *Yuncker et al. 6023* (GH,MO). **Nicaragua. Jinotega:** *Standley 9966, 10730* (F). **Jinotega-Matagalpa:** *Bunting & Licht 972* (GH,NY,US). **Matagalpa:**

L. O. Williams et al. 23874 (F,NY,US). **Zelaya:** *Proctor et al. 27359* (NY). **Costa Rica. Guanacaste:** *Standley & Valerio 46175* (GH); *White & Lucansky 196869, 196873* (DUKE,GH). **Alajuela:** *Brenes 19225* (F); *Burger & Stolze 5100* (GH); *Molina et al. 17158* (F); *Nisman 69, 70* (GH); *White & Lucansky 196876* (DUKE,GH). **Heredia:** *Burger & Stolze 5811* (GH); *Nisman 52, 91, 120, 178* (GH); *Scamman 7002* (GH,US), *7440* (GH); *Scamman & Holdridge 7863* (GH). **Limon:** *Gastony & Gastony 777, 784* (GH); *Kupper 11* (M); *Nisman 132, 137* (GH); *Tonduz 14571* (NY). **San José:** *Brade 213* (A,UC); *Gastony & Gastony 751, 752* (GH); *Kupper 1401* (M); *Molina et al. 18098* (F); *Nisman 39* (GH), *42* (GH sheet 2); *Scamman 5878* (F,GH,NY,UC); *Stork 3117* (UC); *Weber 6085* (GH); *White & Lucansky 1968122* (DUKE,GH). **Cartago:** *Chrysler 5367* (UC); *Chrysler & Roever 5367 pars* (MO); *Gastony & Gastony 775, 788* (GH); *Holm & Iltis 178* (A,F,MO,NY); *Nisman 16, 25, 129, 153* (GH); *Scamman 5886, 7598* (GH), *7001* (GH,US); *White & Lucansky 1968159* (DUKE,GH). **Puntarenas:** *Burger & Stolze 5518* (GH); *de la Sota 5230* (US); *Lent 445* (GH); *Nisman 86, 142* (GH); *White & Lucansky 1968198* (DUKE,GH); *L. O. Williams et al. 28778* (F). **Panama. Chiriqui:** *Cornman 1043* (UC); *Maxon 5078* (GH,MO,NY,US). **Colon:** *Pittier 3904* (GH,NY,US). **Canal Zone:** *Aviles 4* (F,US); *Kenoyer 6* (GH,US). **Panama:** *Cornman 655* (MO,UC); *Killip 2692* (GH,UC,US), *2741* (US). **Ecuador:** 1905, *Sodiro* (MO). **Pichincha:** *Bell 258* (GH); *Sparre 13831* (GH). **Chimborazo:** *Spruce 5744* (F,P). **El Oro:** *Little 6651* (F).

18. **Nephelea polystichoides**

(Christ) Tryon, Contrib. Gray Herb. 200: 40. 1970.

FIGS. 95–98, MAP 24

Alsophila polystichoides Christ, Bull. Soc. Bot. Belg. **35** (Mém.): 177. 1896. TYPE: Costa Rica, "arborescent" Pentes boisées au dessus d'Aragon, 600 m., 20 Oct. 1894, *Pittier 9017*, BR! (annotated as n. sp. Christ but not as herb. Christ, two sheets), photo BM!, probable portion NY! ex Christ; isotypes: NY!, US! (two sheets).

Cyathea polystichoides (Christ) Domin, Pterid. 263. 1929.

Cyathea hastulata Christ, Bull. Herb. Boiss. II, **4**:945. 1904. TYPE: Costa Rica, Arias Agua Punta, *Wercklé s.n.*, P! in herb. Christ; isotype: NY! ex herb. Christ.

Cyathea Werckleana Christ, Bull. Herb. Boiss. II, **6**:181. 1906. LECTOTYPE: Costa Rica, La Palma, 1459 m. (erroneously published as 1495 m.), *Tonduz 12677*, P!; isolectotypes: B!, US! (two sheets). Isosyntypes: *Tonduz 12528*, B!, K!, MO!, NY! (two fragments, one ex K and the other ex US), P! (two sheets), US! (two sheets).

Cyathea hemiotis Christ, Bull. Herb. Boiss. II, 6: 182. 1906. TYPE: Costa Rica, Navarro La Luna, *Werklé*, "arbre élevé, épineaux," whereabouts unknown, perhaps BR. Authentic material which may serve to fix the application of the name until the holotype is located is at BM! (two sheets in herb. Christensen ex herb. Christ), NY! (one sheet ex herb. Christ, one ex Rosenstock, *Werklé* P! (two sheets in herb. Bonaparte), US! (two sheets ex herb. Christ).

Stem to 6 m. tall and 10 cm. in diameter, bearing brown scales especially toward the apex and blackish spines to 5 mm. long, occasionally with adventitious buds. *Unexpanded croziers* with blackish spines to 10 mm. long and brown scales with a dark apical seta to ca. 0.5 mm. long and occasionally with additional smaller apical and lateral setae. *Petiole* to 1 m. long, brown, with blackish spines to 11 mm. long, the scales on the abaxial surface sparingly persistent, brown to tan with a darker central stripe and with a dark apical seta to 0.5–1.0 mm. long and occasionally with several smaller apical and lateral setae. *Lamina* papyraceous to rigidly papyraceous, to ca. 2 m. long and 1.6 m. wide, tripinnate (predominantly bipinnatifid-pinnatifid) to predominantly tripinnate-pinnatifid, abruptly reduced to a distinct pinna-like apex (to 48 cm. long). *Rachis* brown, adaxially pubescent to glabrescent, abaxially furfuraceous-glabrescent. *Central pinnae* sessile to short (to ca. 2 cm.) petiolulate, ovate-lanceolate, to 82 cm. long and 28 cm. wide; *basal pinnae* more or less reduced, to 30–45 cm. long; *pinna-rachis* adaxially pubescent, abaxially furfuraceous-glabrescent,

pubescent distally, with inconspicuous to occasionally conspicuous lateral pneumatodes at the axils of the tertiary axes, narrowly (to ca. 0.4–0.7 mm. wide on each side) greenish-alate between the more distal sessile pinnules. *Pinnules* to 15.5 cm. long and 4.5 cm. wide, predominantly pinnatifid (pinnate at the base) to predominantly pinnate–pinnatifid, sessile to short (to ca. 2 mm.) petiolulate, ovate to elliptic-oblong to obovate, the apex acute to acuminate; *tertiary axis* adaxially pubescent, abaxially furfuraceous-squamose to glabrescent, sparsely pubescent distally, the scales to ca. 2 mm. long, tan, with several dark apical and lateral setae, infrequently clustered in the axil, alate between some to all of the tertiary segments (occasionally pinnules and/or tertiary segments deciduous). *Tertiary segments* straight to sub-falcate or falcate, serrate-crenate (with or without an acroscopic basal auricle) to pinnatilobate or pinnatifid and then sessile to short (to ca. 0.5 mm.) petiolulate, apex subentire to serrate-crenate, margins slightly or not revolute; *quaternary axis* adaxially usually with one to few stiff trichomes distally, occasionally glabrous, abaxially glabrescent to sparsely pubescent distally and sparsely and obscurely squamulose proximally, the squamules light tan, to ca. 0.5 mm. long, dark-setate or with non-dark trichomoid processes, in pinnatilobate to pinnatifid tertiary segments the quintary axes occasionally with a stiff trichome distally on the adaxial surface; *veins* in serrate-crenate margined tertiary segments once or more forked (at or near the quaternary axis), in pinnatilobate to pinnatifid tertiary segments simple on the quintary axes, evident on both surfaces, adaxially glabrous or with an occasional trichome, abaxially glabrous or (especially in tertiary segments) with a diminishing continuation of the indument of the costule; *lamina surface* adaxially and abaxially glabrous between the veins. *Sori* at or near the quaternary axis; *indusium* sphaeropteroid to sub-sphaeropteroid, with or without an apical umbo, diaphanous to whitish tan, of delicate to very delicate texture, usually fugacious at maturity or upon drying of the sorus, often only a remnant remaining around the base of the receptacle, glabrous or nearly so; *receptacle* globose, inserted before loss of the indusium, with short (to ca. 0.1–0.2 mm. long) mostly inconspicuous paraphyses.

In the protologue of *Cyathea Werckleana*, Christ cited at least three collections: La Palma, 1495 m. *Tonduz 12528, 12677*, and Navarro, *Wercklé*. In his search for types at P in 1969, Rolla Tryon could find no material of the *Wercklé* collection in Christ's herbarium, nor have I seen such label data on any sheet with this name from Christ's herbarium. The isolectotype of *Tonduz 12677* at B was unidentified and bears no mark to indicate that Christ ever saw it. The two isolectotype sheets at US are annotated as determined by Christ, but bear the apparently unpublished epithet "pinnula" in the genus *Alsophila*. Two sheets of *Tonduz 12528* were found at P, but neither is stamped as belonging to Christ's herbarium. One is annotated "*Cyathea Werckleana* n. sp.," the other "*Cyathea (Hemitelia)*" with the apparently unpublished epithet "pinnatilobula." The B sheet of *Tonduz 12528* was unidentified; the other isosyntypes are annotated "pinnatilobula," as is an NY sheet from Christ's herbarium *Wercklé* in 1903 without locality. All collections I have seen of *Tonduz 12528* and *12677* which indicate the altitude give 1459 m. rather than 1495 m. as published by Christ, presumably in error. All of this material represents one taxon and may be taken as authentically representing the name. Because the only sheet I have seen from Christ's herbarium bearing the annotation "*Cyathea Werckleana* n. sp." is the *Tonduz 12677* sheet at P, this collection is chosen as the lectotype.

In his search for types at P in 1969, Rolla Tryon was unable to find the

type collection of *Cyathea hemiotis* Christ. The sheets at BM, NY, P, and US cited above as authentic material do not bear the locality data of the type. I have seen no collection from Christ's herbarium which would have provided him with the petiole characters cited in the protologue. It is obvious that the holotype consists of other material at P, BR or elsewhere bearing Wercklé's locality data and forming a more complete specimen.

In the complexity of its lamina, *Nephelea polystichoides* is the most variable species in the genus. Nevertheless, the former recognition of at least three species on the basis of degree of lamina complexity cannot be supported. Whereas no critical characters have been found to justify the recognition of several taxa within *N. polystichoides*, a number of characters indicate that all plants in this taxon form a close genetic alliance. The spines and scales of the petiole base are similar in all specimens. In all forms, the axis of the third order is alate between some or all of the segments of the third order, and the basiscopic pinnules are often acute at the apex whereas adjacent acroscopic pinnules are acuminate. The lamina indument is similar throughout *N. polystichoides*, as are the soral and indusial characters, and in all there is a tendency for the dried segments of the second and third orders to be deciduous. Although the full range of variation of lamina complexity from bipinnate-pinnatifid to tripinnate-deeply pinnatifid has not been observed in any one individual, many specimens do feature much of this variation and their respective ranges of variation overlap from one extreme of the species variation to the other. Finally, all forms occur within the same limited geographic range in Costa Rica and Panama. Available data does not substantiate separation of these forms on the basis of ecology or maturity of the individual.

Nephelea polystichoides evidently shares a close common ancestry with *N. mexicana*, which is itself a rather variable species in its lamina architecture. Adequate materials of these two taxa are clearly separable on the basis of the key characters. Although *N. mexicana* is interpreted in the key as having "tertiary axes not alate between the tertiary segments," the pinnules of some individuals are characterized by sub-basal segments decurrent to the basal segments. These are distinct from, but suggestive of, the condition in *N. polystichoides* noted in the key as "tertiary axes alate between some or all of the tertiary segments."

Nephelea polystichoides is known from the provinces of Alajuela, Heredia, San José, Cartago, and Puntarenas in Costa Rica and from the province of Chiriqui in Panama. It occurs on mountain slopes and along stream banks in undisturbed and cutover cloud forest at altitudes of ca. 700–1970 m. (with one collection recorded as 90 m.).

ADDITIONAL SPECIMENS EXAMINED: **Costa Rica.** 1901–1905, *Wercklé* (NY), 1903, *Wercklé* (NY), 1907, *Wercklé* (P,US), *Wercklé 49,55* (US). **Alajuela:** *Burger & Stolze 5100* (GH); *Gastony & Gastony 793* (GH); *Nisman 72, 79* (GH); *Scamman 7587* (GH,NY,UC,US); *A. Smith H322* (F); *Tonduz*, Herb. Jim. no. 909 (F,US); *White & Lucansky 196810, 196820* (DUKE,GH). **Heredia:** *Burger & Stolze 5811* (GH); *Scamman & Holdridge 7865* (GH). **San José:** *Brade 259* (M,NY,UC,US); *Burger & Stolze 4869*

(GH); *Gastony & Gastony 770* (GH); *Nisman 94, 96* (GH); *Scamman & Holdridge 7866* (GH,US); *Tonduz 2244* (US); *Wercklé*, Herb. Jim. no. 553. 561 (US). **Cartago:** *Kupper 778* (M); *Nisman 26, 28, 126, 151, 154* (GH); *Scamman 7586* (GH); *Tryon & Tryon 6990, 7021, 7037, 7038, 7040, 7041, 7042* (GH); *White & Lucansky 196860, 196862, 196897, 196899, 1968109, 1968132, 1968133, 1968134, 1968140, 1968143, 1968144* (DUKE,GH). **Puntarenas:** *Burger & Stolze 5518* (GH); *Nisman 141* (GH). **Panama. Chiriqui:** *Cornman 1359* (MO,US); *Killip 5393* (US); *Maxon 5706* (GH,NY,US).

DUBIOUS AND EXCLUDED NAMES

Alsophila fulva Mart. & Gal. Mém. Acad. Brux. **15**:78, t. 23. 1842.=*Cyathea fulva* (Mart. & Gal.) Fée, Mém. Fam. Foug. 9:34. 1857. Contrary to Maxon's suggestion (1909), the type of this name (Galeotti 6346 P!) is not a form of *Nephelea mexicana* (Schlect. & Cham.) Tryon, but rather a species of *Cyathea*.

Cyathea glauca Fourn. Mex. Pl. **1**:135. 1872, not Willd. Sp. Pl. **5**:493. 1810. The type collection, *Bourgeau 2794*, is from Mexico and consists of at least the two taxa, *Nephelea mexicana* (Schlect. & Cham.) Tryon and *Sphaeropteris horrida* (Liebm.) Tryon. By Tryon's lectotypification (1971), Fournier's name is excluded from *Nephelea;* it becomes a synonym of *Sphaeropteris horrida* (Liebm.) Tryon.

Cyathea hexagona Fée et Schaffn. ex Fée, Mém. Fam. Foug. 8:111. 1857. TYPE: Mexico, pres Huatusco, *Schaffner 237*. Hooker (1865, in Hooker & Baker) and Maxon (1909) cited this as a synonym of *C. mexicana* Schlect. & Cham. The sterile element of the mixed collection comprising the sheet at K! (in Moore's herbarium ex Fée) is *C. mexicana*. The description of the soral position, the unarmed nature of the trunk, and the reference to scales but not to spines on the petiole in the protologue, however, agree with the fertile element which is a species of *Cyathea* from Mexico and should be the lectotype. I therefore exclude from this name the sterile element which is *Nephelea mexicana* (Schlect. & Cham.) Tryon.

Cyathea Imrayana var. *subnudata* Hook. Sp. Fil. **1**:18. 1844. This variety is excluded from *C. Imrayana*. It is from Jamaica and was collected by Wiles and by Bancroft. It may be a synonym of *C. Tussacii* Desv., but its precise disposition must await a study of the types, presumably at K.

Cyathea mexicana var. *boliviensis* Rosenst. Fedde Repert. **25**:56. 1928. TYPE: Bolivia, Hacienda Simaco supra Tipuani, 1400 m. alt., 3, 1920, *Buchtien 5140*, isotypes: F!, GH!, NY!, US!. This is certainly not a variety of *Nephelea mexicana* (Schlect. & Cham.) Tryon, but rather a species of *Cyathea*.

Alsophila nitens J. Sm. ex Grisebach, Fl. Br. West Ind. 705. 1864. (J. Sm. Lond. Jour. Bot. **1**: 667. 1842. nom. nud.). Although Grisebach cited *Wright 951* among the syntypes and although one of the six sheets of *Wright 951* I have seen is *Nephelea woodwardioides* var. *cubensis* (GH!), *A. nitens* J. Sm. ex Grisebach should be excluded from *Nephelea*. The other five sheets of *Wright 951* I have seen and *Wright 1061* (also cited by Grisebach) are *Cyathea aquilina* Christ, vel aff. *Wright 951*, which is *N. woodwardioides* var. *cubensis*, should not be chosen as the lectotype collection because *N. woodwardioides* var. *cubensis* does not occur in the British West Indian Islands, from which Grisebach described *A. nitens* and because its indusium is not consonant with Grisebach's description.

Cyathea papyracea Christ, Bull. Herb. Boiss. II, 4: 946. 1904. I have seen two sheets from Christ's herbarium at P bearing the annotation *Cyathea papyracea* n. sp. and labeled "1^{ere} feuille" and "2eme feuille." These are clearly two distinct taxa, the first sheet is *Nephelea mexicana* (Schlect. & Cham.) Tryon and the second sheet is a species of *Cyathea*. The second sheet is chosen to represent the name because of the greater correspondence of its indusia and rachis with the description. In addition, Maxon (1909) said the fragment he had seen is close to *C. onusta* Christ, which certainly applies better to the second than to the first sheet, and finally only the second sheet actually bears the identifying *Wercklé 52*. The first sheet is therefore excluded from the type of this name.

Cyathea Sprucei var. *squamosa* Bosco, Nu. Giorn. Bot. Ital. n. ser. 45:142. 1938. Syntypes: Ecuador, in Plan de Milagro, 1500 m. et de Sapote, 2000 m., *Crespi* herbarium del Liceo Pareggiato "Don Bosco" a Torino (Turin), not seen. If this

variety is correctly referred to *C. Sprucei* Hook., it is probably a synonym of *Nephelea incana* (Karst.) Gastony.

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THE BIOSYSTEMATICS OF THE GENUS THELYPODIUM (CRUCIFERAE)

IHSAN A. AL-SHEHBAZ[1]

INTRODUCTION

Those familiar with the Cruciferae readily agree that among the most acute and frequently faced problems in the systematics of this family are those having to do with generic delimitation. It is often claimed that the genera of the Cruciferae are not natural, but perhaps the problem may be better expressed by stating that the generic boundaries are sometimes artificially drawn. Undoubtedly one of the most controversial aspects of the systematics of the family involves its classification into tribes and subtribes. There is little agreement between the 15 or more classifications consulted as to the number of tribes recognized or in the number of genera assigned to a given tribe. This is particularly true of the tribal disposition of the various primitive genera of the family. The two most recent treatments of the Cruciferae (Schulz, 1936; Janchen, 1942) place the ten related primitive genera and their segregates in four to seven tribes. Neither of these is natural nor can they be accepted.

The species dealt with in the present detailed study belong to the genus *Thelypodium* and other closely related genera. They were investigated earlier by Payson (1922, 1923). His treatment helped significantly to establish the proper generic boundaries between *Thelypodium* and *Caulanthus*, but he did not solve the generic placement of certain species that have been referred to *Thelypodium* at one time or another. Furthermore, he (1922) did not satisfactorily treat four species of the alliance by placing them in *Sisymbrium*. Shortly after his two treatments, the species he excluded from *Thelypodium* reappeared in the genus again in some of the major floristic books on western United States. The treatments of Jepson (1936) and Schulz (1936) strongly diverge from that of Payson (1923). Schulz recognized *Thelypodium* as a monotypic genus and maintained all of its previously proposed generic segregates, while Jepson preferred a much broader generic concept. He included in *Thelypodium* species that are generally placed in *Streptanthella* and *Caulanthus*. In addition to the difficulties encountered in establishing the generic boundaries of *Thelypodium*, the tribal classification of the genus has been even more problematic. The genus was placed in the tribes Thelypodieae (Prantl, 1891), Hesperideae (Schulz, 1936) and Sisymbrieae (Janchen, 1942).

The present research consists of a number of approaches, including chemical and palynological, which have not been used before in the study

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of the primitive Cruciferae. This investigation consists of the following: (1) a systematic treatment of *Thelypodium;* (2) establishment of the generic boundaries between the primitive genera of the family as well as their tribal classification; (3) a presentation of some of the evolutionary trends among these primitive genera; (4) palynological analysis of the various species of *Thelypodium* as well as selected genera of the subfamily Cleomoideae-Capparaceae using the scanning electron microscope; and (5) the presentation, for the first time, of a major chemosystematic study of *Thelypodium* involving the distribution of mustard oil glucosides on inter- and intraspecific levels. In this, both paper and gas-liquid chromatographic approaches were utilized.

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I wish to express my thanks and appreciation to the directors and curators of the various herbaria for the loan of specimens. The abbreviations of these herbaria, used for the cited specimens, are those listed by Lanjouw and Stafleu (1964). The field work was financially supported by grants (NSF Grants Nos. GB 3167 and GB 7346 (Professor Reed C. Rollins, Harvard University, Principal Investigator)) to the Evolutionary Biology Committee, Harvard University, the Fernald Fund of Harvard University, and the Society of Sigma Xi.

Last, but certainly not the least, I would like to express my deepest appreciation and gratitude to the Iraqi Government for financial support throughout my entire graduate studies.

History of the Genus

During the earlier stages of botanical exploration of the New World, particularly the last part of the eighteenth and the early decades of the nineteenth centuries, plant specimens were mostly sent to European taxonomists for study. The new species discovered were often matched with known species that belong to Old World genera, and in many instances they were placed in these genera. This was the case with the first species of *Thelypodium* discovered.

In 1830 Sir William Jackson Hooker described a new species of Cruci-

ferae collected by David Douglas near Wallawallah and Priest's Rapids on the Columbia River in what is now the state of Washington. The species was given the name *Macropodium laciniatum. Macropodium* was then known to consist of a single eastern asiatic species, *M. nivale*. Following his discussion on *M. nivale*, Hooker (1830a) wrote the following on *M. laciniatum:* "In the long spiked *raceme* and the general structure of the *flowers*, this has a very close affinity with the preceding species; but there the affinity ceases: for, even in the inflorescence, when it comes to be minutely examined, a very marked difference will be discovered." Hooker then discussed a number of differences in the petals, anthers, pedicels, and gynophores of the two species.

The first attempt to place this American species in a distinct genus was made by Nuttall in his manuscript published by Torrey and Gray (1838). He proposed the name *Pachypodium* to include, in addition to *P. laciniatum*, two new species, *P. integrifolium* and *P. sagittatum*. These three species have been consistently placed in the same genus by most taxonomists even though the generic position of the last species was questioned by Torrey and Gray (1838) who suggested that *P. sagittatum* may belong to *Sisymbrium* section *Cardaminopsis*. The name *Pachypodium* of Nuttall was illegitimate because it was a later homonym to that of Lindley (1830) in the Apocynaceae as well as to *Pachypodium* of Webb and Berthelot (1836) in the Cruciferae. It was replaced by *Thelypodium*, a name proposed by Endlicher (1839). These three species were transferred from *Pachypodium* to *Thelypodium* three years after the publication of the latter genus.

In 1871 Sereno Watson transferred certain species originally described in *Streptanthus* to *Thelypodium*. The generic limits of *Thelypodium* were further expanded by Robinson (1895) to include 23 species. Robinson recognized the heterogeneity of such an assemblage and attempted to reorganize the genus by dividing it into the three subgenera: Hesperidanthus (one species), Heterothrix (two species), and Euthelypodium (20 species).

In 1907 Per Axel Rydberg raised the first two subgenera of Robinson to the rank of genus and proposed three additional genera, *Pleurophragma* (three species), *Stanleyella* (one species), and *Thelypodiopsis* (four species) which he segregated from *Euthelypodium* of Robinson. Rydberg added two species to *Thelypodium* (*T. palmeri* and *T. leptosepalum*) and one to *Pleurophragma* (*P. platypodum*), but it is now clear that they represent a renaming of species previously named by others. A critical evaluation of these segregate genera is presented in the section on the generic limits of *Thelypodium*. In his second edition of the "Flora of the Rocky Mountains and Adjacent Plains," Rydberg (1923) assigned ten species to *Thelypodium*, the first five of which belong to one species, *T. sagittatum*.

Payson (1923) presented a good taxonomic treatment of *Thelypodium* and its immediate allies that helped to establish the generic lines between *Thelypodium, Caulanthus, Streptanthella, Chlorocrambe,* and *Warea.* He gave a critical evaluation of some of Rydberg's segregate genera, but his treatment has a few inadequacies. In my opinion, Payson mistakenly recognized *Stanleyella* as a distinct genus from *Thelypodium* using the orientation of the sepals and the cellular pattern of the septum as a basis for distinguishing the two. Furthermore, he ignored a number of species originally described in *Thelypodium* and did not attempt to discuss their generic status. Payson recognized three species related to *T. integrifolium* (*T. lilacinum, T. affine,* and *T. rhomboideum*), but taxonomists that subsequently dealt with this complex were in fair agreement that a single polymorphic species is involved (Jepson, 1936; Abrams, 1944). One of the strong points in Payson's treatment is his transfer of four species commonly placed in *Thelypodium* to *Caulanthus,* but it is unfortunate that he did not present more convincing reasons for transferring these species (*C. cooperi, C. lasiophyllus, C. flavescens,* and *C. anceps*) because this undoubtedly is the proper generic position for them. In any case, it is surprising to see some or all these four species placed back in *Thelypodium* (Jepson, 1936; Abrams, 1944; Munz, 1959; Hitchcock, 1964).

In 1922 Payson transferred four species known for a long time in *Thelypodium* to *Sisymbrium* (*T. ambiguum, T. elegans, T. aureum,* and *T. linearifolium*) even though he admitted that such a transfer would expand the limits of the latter genus beyond what was then generally recognized.

In 1933 O. E. Schulz transferred a few species from *Thelypodium* to *Thelypodiopsis* and in 1936 he recognized the former genus as monotypic. This was probably because he accepted all the genera segregated from *Thelypodium* by Rydberg and Greene. However, his treatment received no recognition from the botanists who dealt with *Thelypodium* in their floristic treatments. Furthermore, Schulz left two species that unquestionably belong to *Thelypodium* (*T. eucosmum* and *T. flexuosum*) unassigned to any genus.

Finally, Rollins (1946, 1957a) added four species to *Thelypodium* (*T. texanum, T. repandum, T. paysonii,* and *T. tenue*) and presented a critical evaluation of the segregate genus *Stanleyella* which helped significantly in establishing the proper generic limits of *Thelypodium.*

Thelypodium and Related Genera

The family Cruciferae is known for two facts to most students of systematic botany. First, it is one of the most natural families of flowering plants, probably because the flowers are in general very conservative structures. It has been suggested that the Cruciferae represents an adap-

tive peak in the evolution of its flowers (Stebbins 1950, 1951). Second, the Cruciferae is one of the most difficult families in terms of the delimitation of genera (Davis & Heywood, 1963; Rollins, 1938b, 1959). It is altogether possible that the difficulties faced resulted from the lack of high extinction rates that families with more easily delimited genera have suffered (Stebbins, 1950). The species in this family are easy to recognize for the most part (Rollins, 1959) and clearly more "natural" than the genera (Stebbins, 1950), but this does not necessarily mean that there are no problems at the species level, nor does it imply that the genera of the family are artificial. In fact, there are a number of well-defined and readily recognized genera in the family. However, problems on the species level are quite pronounced in genera like *Cakile* (Dr. James E. Rodman, personal communication) and *Isatis* (Davis, 1964; Davis & Heywood, 1963).

The generic limits of *Thelypodium* have been the subject of a continuous controversy. There has been a lack of agreement among the taxonomists who have dealt with this genus in terms of the number of species assigned to it. The number has varied from one species according to Schulz (1936) to 14 (Payson, 1923) and 23 (Robinson, 1895). *Thelypodium* is said to contain 45 species according to Willis' Dictionary of Flowering Plants, while over 70 binomials are listed under the genus in Index Kewensis and the Gray Index. The various species that have been placed in *Thelypodium* by one author or another have fluctuated between a total of at least 20 generic names. Some of these "genera" are nothing but segregates based on minor morphological characters. In the present treatment 18 species, two of which are new, and seven subspecies are recognized. Table 1 summarizes the generic disposition of 31 species as recognized in six major treatments of *Thelypodium* and its allies. It clearly shows that the largest number of segregate genera in this complex were recognized by Schulz (1936) and Rydberg (1907, 1923), while both Robinson (1895) and Jepson (1936) preferred a much broader generic concept.

Thelypodium. The generic limits of *Thelypodium*, as recognized in the present treatment, are essentially the same as those of Payson (1923) with a single exception. Payson recognized the segregate genus *Stanleyella* which here is merged with *Thelypodium*. Rydberg (1907) segregated *T. wrightii* as a genus (*Stanleyella*) mainly on the basis of spreading to reflexed sepals which are erect in *Thelypodium*. He claimed that the glands in *T. wrightii* are inconspicuous as compared to the well-developed glands of *Thelypodium* but admitted that this species is "close to the typical Thelypodia" in its siliques, flowers, and habit. The difference in the glandular tissue, as presented by Rydberg, is unrealistic. Furthermore, the orientation of the sepals within *Thelypodium* is variable. The sepals in *T. laxiflorum*, a very close relative of *T. wrightii*, vary from erect

TABLE 1. THE PLACEMENT OF SPECIES IN THELYPODIUM AND SOME OF ITS SEGREGATES OR RELATED GENERA AS RECOGNIZED BY SIX AUTHORS

Genus	Robinson 1895	Rydberg 1907, 1923	Payson 1922, 1923	Jepson 1936	Schulz 1936	Present Treatment
Thelypodium Endl.	1, 4–11, 13–16, 18–23 (23)	2, 5, 10, 13 (10)	1, 3–10 (14)	1, 4, 6–9, 17–21 (11)	1 (1)	1–12, 26–31 (18)
Stanleyella Rydberg		11 (1)	11 (1)		11 (1)	
Pleurophragma Rydb.		6 (3)			6 (4)	
Streptanthella Rydb.		17 (1)	17 (1)		17 (1)	17 (1)
Hesperidanthus Rydb.		16 (1)			16 (1)	
Pennellia Nieuwland (Heterothrix Rydberg)		22, 23 (2)			23 (6)	22, 23 (?)
Thelypodiopsis Rydb.		14, 15, 24, 25, (5)			3–4, 7–8, 10, 12, 14–15, 26 (14)	13–16, 24–25 (6)
Sisymbrium L.			13–16, 24, 25			
Caulanthus Watson			18–21 (18)			18–21 (15)
Microsisymbrium Sch.					18 (6)	
Lamprophragma Schulz					22 (1)	
Guillenia Greene					19, 21 (4)	

Numbers in parenthesis are the total number of species recognized by the author in that genus. 1. *Thelypodium laciniatum*, 2. *T. milleflorum*, 3. *T. crispum*, 4. *T. brachycarpum*, 5. *T. eucosmum*, 6. *T. integrifolium*, 7. *T. stenopetalum*, 8. *T. howellii*, 9. *T. flexuosum*, 10. *T. sagittatum*, 11. *T. wrightii*, 12. *T. paniculatum*, 13. *Thelypodiopsis ambigua*, 14. *T. elegans*, 15. *T. aurea*, 16. *T. linearifolia*, 17. *Streptanthella longirostris*, 18. *Caulanthus lasiophyllus*, 19. *C. flavescens*, 20. *C. anceps*, 21. *C. cooperi*, 22. *Pennellia longifolia*, 23. *P. micrantha*, 24. *Thelypodiopsis juniperorum*, 25. *T. wyomingensis*, 26. *Thelypodium texanum*, 27. *T. repandum*, 28. *T. tenue*, 29. *T. paysonii*, 30. *T. rollinsii*, 31. *T. laxiflorum*.

to spreading. The former species was treated as a variety of the latter by Payson. Spreading and erect sepals are known in a number of genera of the Cruciferae. This is particularly true in *Caulanthus*, *Brassica*, *Sisymbrium*, *Leavenworthia*, and some others. It is the writer's strong feeling that one character difference is not enough to provide the basis for segregating a genus, particularly if there is some doubt of its value or consistency. It is very clear, as pointed out by Rollins (1957a), that the segregate genus *Stanleyella* does not deserve independent recognition.

Pleurophragma of Rydberg (1907) was based on the single character of the septum which was said to possess a "strong and broad midrib," while the species of *Thelypodium* were not supposed to have a distinct midvein. Not only was this character seriously questioned by Payson (1923), but it was found to be unreliable and inconsistent. I have studied the various aspects of the septum throughout the genus and failed to recognize any features of taxonomic value. Therefore, *Pleurophragma* does not merit recognition.

Thelypodiopsis. Controversy still exists as to whether *Schoenocrambe* Greene, *Thelypodiopsis* Rydberg, and *Hesperidanthus* Rydberg should be maintained as separate genera or merged with *Thelypodium* or *Sisymbrium*. *Hesperidanthus* is based on a single species, *H. linearifolius*. The main difference between this species and the true members of *Thelypodium* is found in the stigma, which is entire and small in species of the latter genus (Plate 1) and conical in *Hesperidanthus*. Both Robinson (1895) and Rydberg (1907) claimed that the stigma in *H. linearifolius* is not lobed, while Payson (1922) and Schulz (1936) stated that it is distinctly bilobed. I have carefully looked at this feature of the stigma on more than 200 herbarium sheets and in no case have I been able to find an entire stigma in this species. On the contrary, it is strongly bilobed with the lobes opposite the replum, firmly touching each other, and almost completely connivent (Plate 1). Because of its stigmas, *H. linearifolius* is very distinct from all the species placed in *Thelypodium* in the present treatment. In its stigma and other morphological aspects, it significantly resembles the species often placed in *Thelypodiopsis*. Therefore, *Hesperidanthus* does not need to be recognized and its single species should be placed in *Thelypodiopsis*.

Thelypodiopsis was segregated from *Thelypodium* by Rydberg (1907) on the basis of having strongly bilobed stigmas (Plate 1) with the lobes opposite the replum. He recognized four species in *Thelypodiopsis* (*T. aurea*, *T. elegans*, *T. wyomingensis*, and *T. bakeri*). In 1923 he added a fifth species by transferring *Sisymbrium juniperorum*. In 1933 Schulz transferred a number of species from *Thelypodium* to *Thelypodiopsis* without giving any reasons supporting his transfers. Three years later (1936) he distinguished the two genera mainly on the basis of having obtuse anthers in the former genus and acute or apiculate anthers in *Thelypodiopsis*. This alleged difference is far from being realistic, since it is very hard to decide in many cases whether the anther is apiculate or not. Furthermore, this feature does not seem to be significant enough to call for such a massive transfer of species. It is quite clear that none of the transferred species fit the concept of *Thelypodiopsis* as defined by Rydberg (1907). Therefore, in the following discussion we use the generic limits of *Thelypodiopsis* as presented by Rydberg rather than those of Schulz. Needless to say, all the species that Schulz transferred from *Thelypodium* to *Thelypodiopsis* are perfectly at home in the former genus.

Payson (1922) did not recognize *Thelypodiopsis* and he transferred its four species to *Sisymbrium*. He recognized 11 species of *Sisymbrium* native to North America north of Mexico, six of which seem to be at home in this genus, but Payson mishandled the nomenclature of two of these species (cf. Rollins, 1960a). The remaining five species (*S. ambiguum*, *S. aureum*, *S. elegans*, *S. juniperorum*, and *S. linearifolium*) make one group of interrelated species, which appear not to be phylogenetically

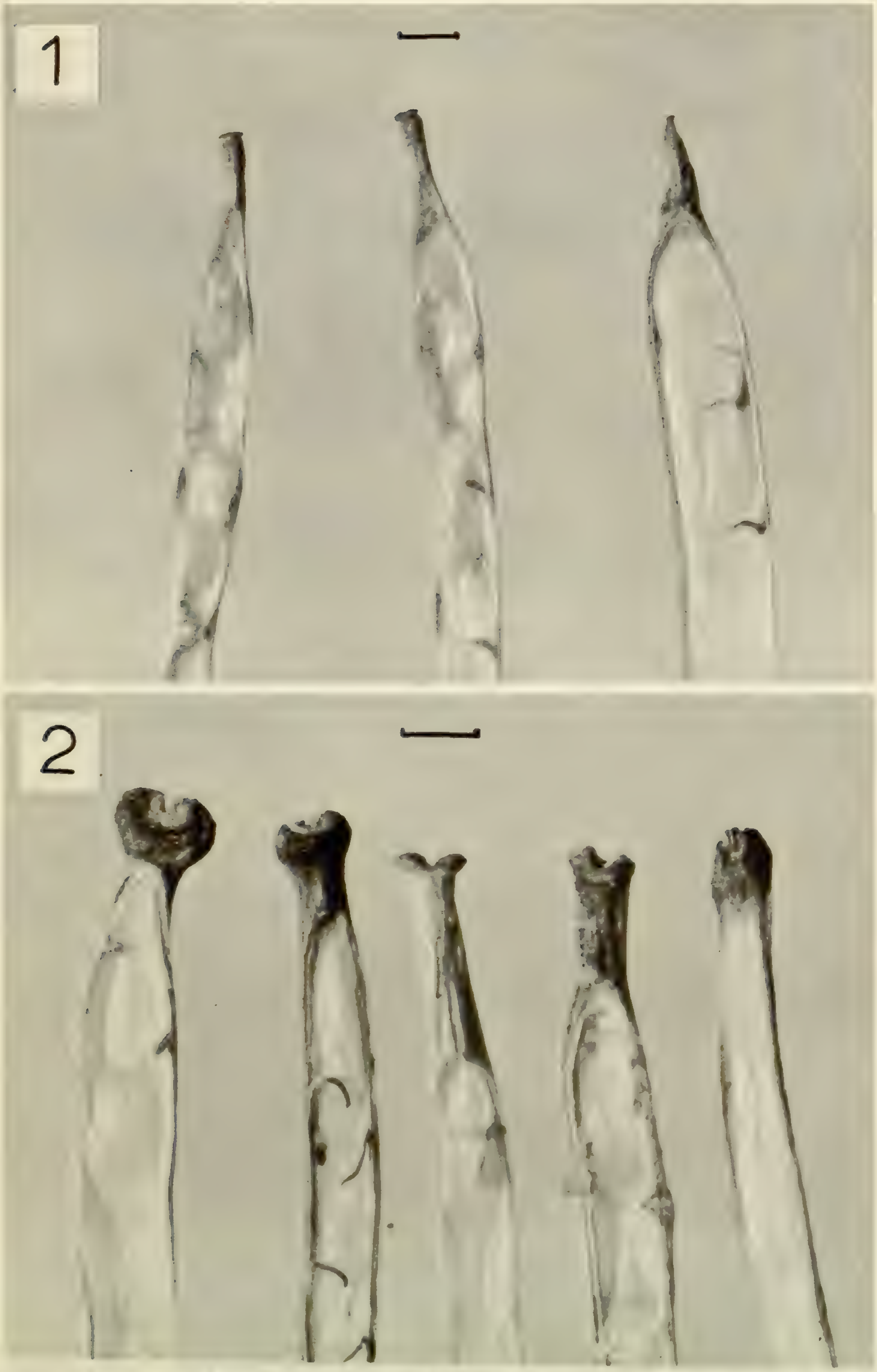


PLATE 1. Stigmas and styles of *Thelypodium* (1) and *Thelypodiopsis* (2). FIG. 1. Left to right: *Thelypodium rollinsii*, *T. wrightii*, and *T. texanum*. FIG. 2. Left to right: *Thelypodiopsis wyomingensis*, *T. ambigua*, *T. juniperorum*, *T. elegans*, and *T. linearifolia*. Scale: one millemeter.

related to any of the species that he maintained in *Sisymbrium*. The present writer strongly feels that these species must not be placed in *Sisymbrium* for the following reasons. First, the presence of a distinct gynophore that can reach a maximum length of 1–1.5 cm. in three of the five species is not found in any species of *Sisymbrium*. The siliques in this genus are almost always sessile or subsessile. Second, two of these five species, *ambiguum* and *aureum*, have other morphological features in the flowers and inflorescences that tie them more with the primitive members of the family. Admitting these species to *Sisymbrium* carries the implication that this genus has to be associated with the primitive genera of the Cruciferae. Such an action is not likely to receive support from botanists familiar with these plants. Third, the chromosome numbers known from two of these five species (*ambiguum* and *linearifolium*) are based on n=11 (Rollins, 1966; Rollins and Rüdenberg, 1971), while 14 out of the 24 species of *Sisymbrium* listed by Bolkovskikh *et al.* (1969) have a haploid number of n=7 and six of the 10 remaining species have higher chromosome numbers, based on x=7. Although our knowledge of the chromosome numbers in this complex is far from complete, the pattern seems to be clear enough to support the exclusion of these five species from *Sisymbrium*. Finally, the close relationship of these five species to each other and not to any known species of *Sisymbrium* or any other genus supports their placement in a genus of their own. Therefore, *Thelypodiopsis* seems to be the best alternative for treating the five species under consideration.

The genus *Schoenocrambe* was segregated from *Sisymbrium* by Greene (1896) on the basis of a single vegetative character (root stock), which is present in S. *linifolium* and lacking in the other species of *Sisymbrium*. He listed two other "species" and Rydberg (1904) added a fourth one, but it is clear, as pointed out by Payson (1922), that a single polymorphic species is involved. *Sisymbrium linifolium* shows some superficial resemblance to certain species of *Thelypodiopsis* in its flowers and siliques. Payson held the view that this species is closely related to what we are calling *Thelypodiopsis linearifolia*, but the two species are very different in their flower morphology. Because S. *linifolium* is not closely related to any species of *Sisymbrium* native in North America, and that it superficially resembles species of *Thelypodiopsis*, creates a problem in terms of its generic disposition. Placing S. *linifolium* with species of *Thelypodiopsis* would mean that *Schoenocrambe* has to be recognized because it was published before *Thelypodiopsis*. However, we strongly believe that S. *linifolium* is more at home in *Sisymbrium* than in *Thelypodiopsis*, and that *Schoenocrambe* is not worth recognition for the following reasons. First, S. *linifolium* appears to be very closely related to a perfectly good *Sisymbrium*, S. *polymorphum* (Murray) Roth. (=S. *junceum*), which is native and widely distributed in Europe (Ball, 1964) and the U.S.S.R.

(Vasil'chenko, 1939). Such a close relationship was pointed out by Greene (1896), Payson (1922), and Schulz (1924). In fact, the last author treated S. *linifolium* directly after S. *polymorphum*, while Payson pointed out that that "the differences are very slight between the American plant and the Asiatic and European S. *junceum* Bieb." Furthermore, plants of S. *linifolium* were misidentified as S. *junceum* by Hooker (1830b) and Nuttall (in Torrey & Gray, 1838). Second, the chromosome number of S. *linifolium* fits very well in *Sisymbrium* as it appears to be based on *n*=7 (Rollins, 1966; Rollins & Rüdenberg, 1971), while *Thelypodiopsis* seems to be based on *n*=11. Third, the lack of a distinct gynophore in S. *linifolium* supports the disposition of this species in *Sisymbrium* and not *Thelypodiopsis*. Finally, the genus *Schoenocrambe* is not recognized because it was based on a vegetative character. Vegetative characters are hardly of significance in establishing generic relationships or limits, nor can they be of major value in classification when used alone (cf. Rollins, 1952, 1957b).

Caulanthus. Four species of *Caulanthus* (*C. lasiophyllus*, *C. flavescens*, *C. cooperi*, and *C. anceps*) have fluctuated back and forth between *Caulanthus* and *Thelypodium*. *Caulanthus lasiophyllus* was transferred to *Thelypodium* by Greene (1886). The four species were recognized in *Thelypodium* for more than 35 years. In 1923 Payson transferred them to *Caulanthus*, where they should be retained.

Caulanthus cooperi presents the fewest problems of the four species. The various aspects of the calyx, petals, and siliques are fairly similar to the typical species of *Caulanthus* and it should always be maintained in that genus. However, Jepson (1925, 1936) treated it as a *Thelypodium* even though he admitted (1936) that it "would rest as well in *Streptanthus*" and that "it might as well be considered a primitive *Streptanthus*." Jepson united *Caulanthus* with *Streptanthus*, an action that I do not support for reasons to be discussed below.

Caulanthus flavescens is no more difficult than *C. cooperi* if one takes the characteristic features of the petals into consideration. In both of these species as well as those central to *Caulanthus*, the petal blades are narrower than the claws and they are crisped or coiled. The claws are differentiated from the blades and they are mostly obovate to oblanceolate. These features of the petals are very important in distinguishing between *Caulanthus* and *Thelypodium* since they are not found in any species of the latter genus. The only two species that deviate from this general pattern are *C. lasiophyllus* and *C. anceps*, but these are properly placed in *Caulanthus* if other characters are taken into consideration (Table 2). Jepson (1936) did note the streptanthoid flowers of *C. flavescens* but he preferred to maintain the species in *Thelypodium* even though he stated that "In *Streptanthus* it seems related to S. *pilosus* Jepson and S. *hallii* Jepson." We believe this species is a *Caulanthus* for the reasons summarized in Table 2.

TABLE 2. COMPARISON BETWEEN SPECIES OF THELYPODIUM AND CAULANTHUS

Character	*C. cooperi*	*C. flavescens*	*C. anceps*	*C. lasiophyllus*	other spp. of *Caulanthus*	spp. of *Thelypodium*
Stem	solid	hollow	mostly hollow	hollow or solid	hollow in 6 spp., solid in 3, hollow or solid in 2	solid in 17 spp., hollow in one
Sepals	glabrous	glabrous or pubescent	glabrous or pub.	glabrous or pubescent	glabrous in one sp., pubescent in 3 spp., glab. or pub. in 7 spp	glabrous in all 18 species
Pedicel	glabrous or pub.	mostly pubescent	glabrous or pub.	glabrous or pubescent	glabrous in one sp., pubescent in 5 spp., glab. or pub. in 5 spp	glabrous in all 18 species
Pedicel orientation	curved, reflexed	strongly curved, erect or reflexed	strongly curved, erect or reflexed	strongly curved, erect or reflexed	slightly to strongly curved, erect, reflexed, or spreading	straight or slightly curved, strongly curved in one sp., variously oriented
Gynophore	1 mm. long, very broad	1 mm. or less, very broad	1 mm. or less, very broad	1 mm. or less, very broad	1 mm. or less, very broad	1–8.5 mm. long in 14 spp., 1 mm. or less in 4 spp., not broad
Stigma	bilobed, lobes opposite valves	bilobed or subentire, lobes opp. valves	bilobed or subentire, lobes opp. valves	entire or rarely slightly bilobed	bilobed in all remaining species, lobes opposite valves in 9 spp., opp. replum in 2 species	entire in all 18 species
Chromosome numbers	$n = 14$	$n = 14$	$n = 14$	$n = 14$	$n = 14$ in 4 species, $n = 10$ in 2 species	$n = 13$ in 9 species

Caulanthus anceps is more of a problem because its flowers do not suggest its generic placement. The spreading nature of the sepals, petals, and stamens of *C. anceps* is also present in five species of *Thelypodium* that also have petiolate cauline leaves. Considering such characters, *C. anceps* could easily be placed in *Thelypodium*. However, if this is done, the species would have no relatives, close or remote, within *Thelypodium*. Rather, its nearest relative would be a species of *Caulanthus*, *C. flavescens*. The various aspects of the siliques, pedicels, sepals, glandular tissue, inflorescence, and, to a certain extent, the leaves of these two species show remarkable similarities. The petals in *C. anceps* are neither crisped nor chanelled or coiled and the blades are attenuate into a narrow and slender claw-like base. *Caulanthus anceps* and *C. lasiophyllus* have recently been treated as *Streptanthus* by Hoover (1966, 1970).

Of the four species of *Caulanthus* discussed above, *C. lasiophyllus* perhaps presents the most problems. One reason is that it does not have the characteristic caulanthoid flowers that are present in most species of the genus. The calyx is not urceolate and the petals are neither crisped nor chanelled. Because of this, the species was, for the most part, excluded from *Caulanthus*. However, there is scarcely any significant morphological evidence that supports its placement in *Thelypodium*. In fact, *C. lasiophyllus* resembles certain species of *Sisymbrium* in some features more than it does those of either *Caulanthus* or *Thelypodium*. Therefore, it is not surprising to find that some of the collections of this species were described as new under such names as *Sisymbrium deflexum*, *S. reflexum*, and *S. acuticarpum*. However, we are retaining *C. lasiophyllus* and its relatives in *Caulanthus* for reasons summarized in Table 2.

Plants of this species grown from seeds of three population samples in the greenhouse showed a remarkably high percentage of autogamy. This was roughly estimated to range between 80 and 100 per cent. A number of floral adaptations to such a mode of reproduction were observed: small flower size, reduced glandular tissue or its absence, enlarged stigmas, reduced anther size. Also, anthers that are found to be dehisced and touching the stigmas before full anthesis seem to be clear adaptations to autogamy. The lack of true caulanthoid characters in the flowers of *C. lasiophyllus* may be related to its breeding system.

In conclusion, I am convinced that the four species of *Caulanthus* discussed in the preceding paragraphs and compared with the remaining species of the genus and *Thelypodium* in Table 2 clearly should be placed in *Caulanthus* and not *Thelypodium*. The content of this table needs no elaboration as the items are self-evident. However, it is perhaps significant that the pubescence on the sepals in *Caulanthus* (including *C. flavescens*, *C. anceps*, and *C. lasiophyllus*) is often made up of very few trichomes restricted to their tips.

The generic limits of *Caulanthus* are somewhat indefinite. Watson (1871)

segregated the genus from *Streptanthus* on the basis of its having terete siliques and incumbent cotyledons instead of the flattened siliques and accumbent cotyledons present in the species of the latter genus. Jepson (1925, 1936) united *Caulanthus* under *Streptanthus* because of the overall similarities in the flower morphology of the two genera. He neglected the differences in the siliques, seeds, and cotyledonary position in relation to the radicle, which are used as the basis for distinguishing the two genera. It is my strong feeling that the two genera should be maintained, and I fully agree with Rollins (1971) that "it is in the interest of a reasonable and workable classification to accept both *Caulanthus* and *Streptanthus*."

Caulanthus seems to be made up of at least 15 species including the recently described *C. divaricatus* (Rollins, 1971). Four of the 18 species recognized by Payson (1923) present some problems. Three species, *C. amplexicaulis*, *C. heterophyllus*, and *C. simulans*, appear to be more properly placed in *Streptanthus* than in *Caulanthus* because they have somewhat compressed siliques, accumbent cotyledons, and a narrow or rudimentary wing at the distal end of the seed. *Caulanthus sulfureus* of Payson is unquestionably *Brassica*. I have seen the holotype of *C. sulfureus* and agree with both Kearney and Rollins in annotating it as *B. campestris*. The exact number of species in *Streptanthus* is not known, but an estimate of 30 to 35 species may not be far off the mark.

Streptanthella. This monotypic genus is based on a species originally described as *Arabis longirostris* by Watson (1871). It was known as a *Streptanthus* for nearly 30 years after its transfer there by Watson (1889). *Streptanthella* was proposed by Rydberg in 1917 and since then the genus has been recognized by the majority of taxonomists who have dealt with its only species. *Streptanthella longirostris* resembles certain species of *Caulanthus* in its flowers, incumbent cotyledons, and the orientation of its siliques, but differs significantly in having flattened siliques that are beaked and by its winged seeds. *Streptanthella* resembles *Streptanthus* in its flattened siliques, winged seeds, and flowers but it differs in having incumbent instead of accumbent cotyledons and its style-like beak with the distal part of the silique often remains indehiscent and contains 2–4 seeds.

The treatment of *Streptanthella longirostris* as a species of *Thelypodium* by Jepson (1925, 1936) is not supported by present morphological evidence. The streptanthoid flowers, winged seeds, beaked siliques, and stamens that occur in three pairs of different lengths are characters not found in any species of *Thelypodium*.

The distinctness of *Streptanthella longirostris* from the closely related genera *Caulanthus* and *Streptanthus* as well as from *Thelypodium* argues for its recognition as a monotypic genus.

Pennellia. Two species of *Pennellia*, *P. micrantha* (Gray) Nieuw. and

P. longifolia (Bentham) Rollins, were originally described as species of *Streptanthus* and later transferred to *Thelypodium* by Watson (1882). Watson's concept of the generic limits of *Thelypodium* was so broad that some of the species he placed in this genus (1871) are currently placed in the genera *Caulanthus, Iodanthus, Pennellia,* and *Thelypodiopsis.* Robinson (1895) was the first to recognize that the two species mentioned above are anomalous in *Thelypodium* and placed them in a subgenus of their own, *Heterothrix,* which was raised to the rank of genus by Rydberg (1907). The name *Heterothrix* Rydberg is illegitimate because, as shown by Nieuwland (1918), it is a later homonym of *Heterothrix* Muell. (=*Echites* L.) in the Apocynaceae. Nieuwland proposed the name *Pennellia* to replace *Heterothrix* of Rydberg. Rollins (1960b) showed that *Thelypodium longifolium* is congeneric with *Pennellia micrantha.*

Pennellia is clearly different and readily distinguishable from *Thelypodium* by a number of morphological features. First, the dendritic trichomes that are mostly present on the lower half of the plants of *Pennellia* are not found in any species of *Thelypodium.* Most species of *Thelypodium* are glabrous and those that are pubescent have only simple trichomes. In addition to the prevalent dendritic trichomes, *Pennellia* has simple trichomes as well. Second, the inflorescence in *Pennellia* is definitely a lax raceme and both the floral buds and flowers are small (generally less than 6 mm. long) and mostly spherical. In *Thelypodium* the inflorescence is racemose or corymbose and usually densely flowered but neither the buds nor the flowers are spherical (mostly oblong) and the flowers may be up to 2 cm. long. Finally, the majority of *Thelypodium* species have exserted stamens, coiled anthers, distinct gynophores, and the petals are differentiated into claw and blade, while the stamens in *Pennellia* are included, the anthers are hardly coiled, the gynophores are mostly obsolete, and the petals are not differentiated into a distinct claw and blade. In fact, the differences between the two genera are so great that *Pennellia* is not particularly related to *Thelypodium.*

Classification of the Primitive Cruciferae

There is general agreement among those of us involved in systematic studies of the various genera of the Cruciferae that none of the proposed systems of classification above the genus level are fully adequate. For reasons to be discussed below, some of the earlier systems, such as those of De Candolle (1821b, 1824), Bentham and Hooker (1862), and Prantl (1891), and some of the more recent ones, e.g., Schulz (1936) and Janchen (1942), fail to provide a natural tribal classification for the primitive genera of the family. The lack of agreement between the main systems in the tribal placement of these primitive genera (Table 3) may have resulted from the use of one or a very few characters as the basis for the tribal divisions rather than grouping the genera on the basis of their relationships to each other.

Our discussion is limited to the genera placed in the tribe Thelypodieae by the present writer and starts from the system of De Candolle (1821b). The tribal classification of the primitive Cruciferae in the treatments of Endlicher (1839), Walpers (1842), Bentham and Hooker (1862), and Baillon (1874) was essentially the same as that of De Candolle (1821a, 1821b, 1824), the main difference being the use of different names above the tribal level by some of these authors and the addition of the genus *Streptanthus* to the tribe Arabideae and *Warea* and *Thelypodium* to the Sisymbriae. The cotyledonary position in relation to the radicle, accumbent versus incumbent, and the nature of the silique are the basic features on which these two tribes are defined in the system of De Candolle. A system that places *Streptanthus* and *Macropodium* in the tribe Arabideae and their relatives *Stanleya, Warea,* and *Thelypodium* in the tribe Sisymbrieae is obviously artificial. *Stanleya* and *Thelypodium* are improperly classified because the former genus has both accumbent and incumbent cotyledons (Rollins, 1939) while the latter has obliquely accumbent to obliquely incumbent cotyledons.

Prantl (1891) differed strongly from De Candolle's system by using the characteristics of the stigmas (capitate versus bilobed) and the trichomes (presence versus absence, simple versus branched) as the basis for his major divisions. He recognized 20 subtribes distributed in the four tribes Thelypodieae, Sinapeae, Schizopetaleae, and Hesperideae. The tribe Thelypodieae was defined to include glabrous plants or those with simple trichomes as well as entire or capitate stigmas. It was divided into four subtribes: Stanleyinae, Cremolobinae, Heliophilinae and Chamirinae. Under the subtribe Stanleyinae, Prantl included the genera *Notothlaspi, Pringlea, Warea, Stanleya, Thelypodium, Caulanthus,* and *Streptanthus.*

The system of Prantl was intended to be natural but in fact, it is no less artificial than that of De Candolle. The nature of the pubescence is hardly of value when used in classifications above the genus level. There are genera with various types of pubescence ranging from simple to branched and even peltate. The best examples are the genera *Lesquerella* (Rollins & Shaw, 1973) and *Arabis* (Rollins, 1941c). The use of trichomes as the basis for tribal classification led to the separation of the genus *Macropodium* to a different tribe (Hesperideae) from its relatives found in the subtribe Stanleyinae-Thelypodieae.

The tribe Thelypodieae, as defined by Prantl, contained an extremely heterogeneous assemblage of genera that show a wide range of diversity in fruit morphology. Only five of the 17 genera placed in Thelypodieae are distributed in the Northern Hemisphere. They are the last five of the subtribe Stanleyinae (Table 3). Prantl believed that the most primitive forms of the Cruciferae are found in the Southern Hemisphere, but we believe this is not the case. All ten genera of the tribe Thelypodieae, as recognized by the present writer, have a Northern Hemisphere distribu-

TABLE 3. TRIBAL CLASSIFICATION OF THE PRIMITIVE CRUCIFERAE

Endlicher, 1839	Prantl, 1891	Hayek, 1911	Schulz, 1936	Present Treatment
Subordo I Pleurorhizeae Tribus I Arabideae *Streptanthus* *Macropodium*	Tribe I. Thelypodieae 1. Subtribe Stanleyinae *Notothlaspi* *Pringlea* *Warea* *Stanleya* *Thelypodium* *Caulanthus* *Streptanthus* 2. Subtribe Cremolobinae 3. Subtribe Heliophilinae 4. Subtribe Chamirinae	Tribe I. Thelypodieae 1. *Stanleya* 2. *Warea* 3. *Macropodium* 4. *Streptanthus* 5. *Euclisia* 6. *Microsemia* 7. *Schoenocrambe* 8. *Caulanthus* 9. *Thelypodium*	Tribe II. Stanleyeae *Stanleya* *Warea* *Chlorocrambe* *Macropodium* Tribe III. Romanschulzieae *Romanschulzia* Tribe IV. Streptantheae Subtribe Euklisinae *Streptanthus* *Streptanthella* *Disccanthus* *Cartiera* *Agianthus* *Mitophyllum* *Microsemia* *Euklisia* *Icianthus* *Pleiocardia* Subtribe Caulanthinae *Caulanthus* *Stanfordia* Tribe XVI. Arabideae (29 genera) *Pleurophragma* *Guillenia* Tribe XVII. Matthioleae (17 gen.) *Hesperidanthus* Tribe XVIII. Hesperideae (20 gen.) *Thelypodium* *Thelypodiopsis* Tribe XIX. Sisymbrieae (74 gen.) Subtribe Sisymbrinae *Microsisymbrium* *Stanleyella*	Tribe *Thelypodieae* 1. *Stanleya* 2. *Warea* 3. *Thelypodium* 4. *Macropodium* 5. *Chlorocrambe* 6. *Romanschulzia* 7. *Thelypodiopsis* 8. *Streptanthus* 9. *Caulanthus* 10. *Streptanthella*
Subordo II Notorhizeae Tribus VII Sisymbrieae *Thelypodium* *Stanleya* *Warea*				
	Tribe IV. Hesperideae Subtribe Turritinae *Macropodium*	Tribe VI. Schizopetaleae Subtribe Schizopetalinae *Stanfordia*		

tion. The most primitive known Cruciferae are among these ten genera (Table 3). *Pringlea* and *Notothlaspi* are neither related to each other nor to other members of the subtribe Stanleyinae. Although *Pringlea* possesses certain features that are present in the truly primitive Cruciferae (such as the exserted stamens and long racemes), these features are very likely to have originated independently. The reduction in petal size, the exserted stamens, and the long and densely flowered racemes are perhaps adaptations to wind pollination which is not known elsewhere in the Cruciferae. The lack of the septum might have been another reason for overestimating the primitiveness of *Pringlea*. However, this feature evidently has evolved several times, independently, within the Cruciferae. All the truly primitive genera have a complete septum. In my opinion, the features of the septum, inflorescence, and flowers in *Pringlea* are derived and the genus is not related at all to those that I place in the tribe Thelypodieae.

Prantl listed *Stanfordia* Watson with 17 other genera of uncertain position at the end of his treatment. He indicated that it possibly belongs to the tribe Schizopetaleae as he apparently followed Watson (1880) in associating the genus with *Tropidocarpum,* which is often placed in this tribe. However, we believe that *Stanfordia californica* is no more than a good species of *Caulanthus*. *Stanfordia* was based primarily on the presence of unusual trifid cotyledons, a feature that Watson overlooked in a species that he described as *Caulanthus coulteri.*

Robinson (1895) presented the best tribal classification of the primitive Cruciferae of North America. He placed the genera in the tribe Stanleyeae, a name that was used on the tribal level for the first time, instead of the earlier published Thelypodieae of Prantl (1891). Stanleyeae was proposed first by Nuttall (1834) as a family including the genera *Stanleya* and *Warea*. The tribe Stanleyeae, as treated by Robinson, was a truly natural assemblage of related genera. However, he maintained *Stanfordia* and listed it between *Streptanthus* and *Caulanthus*.

In 1911 Hayek presented a system of classification for the whole family. He adopted the tribal name Thelypodieae to include, with the exception of *Schoenocrambe,* all the known primitive genera of the family. However, he probably overlooked the work of Rydberg (1907) since he did not mention any of the segregates of *Thelypodium,* or *Chlorocrambe*. The placement of *Schoenocrambe* with the primitive crucifers is not justified for reasons mentioned above. There are three other points of weakness in Hayek's classification. First, he recognized *Euclisia* and *Microsemia* that were segregated from *Streptanthus* by Greene (1904). We believe that these are not worth recognition. Second, he derived *Caulanthus* and *Streptanthus* from totally different ancestors. *Caulanthus* and *Thelypodium* were said to be derived from *Schoenocrambe* while *Streptanthus* was derived from *Warea* and both *Warea* and *Schoenocrambe*

were derived directly from *Stanleya*. *Caulanthus* and *Streptanthus* are so similar to each other in their floral morphology that their generic limits are often confused and the boundaries between them are hard to define. It is difficult to visualize the independent origin of such remarkable flowers from ancestors that are extremely different from each other and from both *Streptanthus* and *Caulanthus*. Third, he placed *Stanfordia*, a genus that we believe to be at home in *Caulanthus*, in the tribe Schizopetaleae. It is probable that Hayek overlooked Robinson's (1895) treatment, since the latter author was the first to associate *Stanfordia* with *Caulanthus*. One significant improvement of Hayek's system over that of Prantl (1891) is the removal of *Notothlaspi* and *Pringlea* to the tribes Schizopetaleae and Pringleae respectively. It is beyond the scope of the present study to evaluate the tribal position of these two genera, but we certainly agree that they are not related to the primitive crucifers.

In 1936 Otto E. Schulz published a comprehensive monograph of the family Cruciferae that includes a number of strong as well as weak points. The detailed descriptions of the tribes and genera supported by illustrations and keys are undoubtedly very useful. However, Schulz has often been criticized for the large number of genera and tribes he recognized and for the placement of certain closely related genera in widely separated tribes. There is no doubt his treatment of the primitive Cruciferae, both on the tribal and generic levels, created more problems and controversy than any other system of classification extant. Our evaluation of his system with regard to these crucifers is presented in the following paragraphs.

As we stated before, the consideration of *Pringlea antiscorbutica* as the most primitive living member of the Cruciferae by Prantl (1891), Schulz (1936), and Janchen (1942) does not seem to be supported by the facts. The tribe Stanleyeae is made up of a natural assemblage of four genera—*Stanleya*, *Warea*, *Chlorocrambe*, and *Macropodium*. Schulz distinguished this tribe from the others by its exserted stamens, long gynophores, and nearly sessile stigmas. Certain species of *Thelypodium*, such as *T. milleflorum*, *T. eucosmum*, and *T. laciniatum*, have distinctly exserted stamens and usually long gynophores that can be longer than those of *Chlorocrambe*. Had Schulz looked at these features carefully in these three species of *Thelypodium*, he would have found that the genus is at home with the other four genera he placed in the Stanleyeae. However, he placed *Thelypodium* in the tribe Hesperideae and this led him to choose a tribal name other than Thelypodieae for the four genera mentioned above. The fact that both *Thelypodium* and *Stanleya* should be placed in the same tribe has been elegantly pointed out by Rollins (1939) in the following words: "O. E. Schulz (1936) has placed *Stanleya* and *Thelypodium* in widely separated tribes of the Cruciferae, but on the basis of observed facts such a disposition is decidedly unwar-

ranted. Insofar as these genera are concerned, the retention of the tribe Thelypodieae of Prantl (1891) as modified by von Hayek (1911) more nearly presents the actual phylogenetic relationships in this group than does the system of O. E. Schulz." Schulz maintained *Thelypodiopsis* and placed it with *Thelypodium* in the tribe Hesperideae. However, neither the generic limits of *Thelypodiopsis* nor its tribal disposition were correctly treated. *Thelypodiopsis* is to be associated with its nearest relatives which we place in the tribe Thelypodieae.

The genus *Romanschulzia* was given a tribe of its own, Romanschulzieae, by Schulz, which was maintained by Janchen (1942). The characters used in defining this tribe are primarily the spreading nature of the floral parts and the insertion of the filament bases in distinct depressions on the receptable. *Romanschulzia* is not the only primitive genus with spreading floral parts. Five species of *Thelypodium*, *Caulanthus anceps*, and all the species of *Stanleya* and *Warea* have spreading parts. Therefore, this character has little value in establishing a tribe for *Romanschulzia*. The filaments in this genus are distinctly dilated at the base and mostly are surrounded by glandular tissue. Upon the removal of the filaments, the glandular tissue appears with six depressions corresponding to the insertion points of the filaments. This feature alone is not strong enough to be used as the sole basis for establishing an independent tribe. Rather, *Romanschulzia* fits very well in the tribe Thelypodieae because it shares a number of features of the flowers, fruits, and inflorescences with other members of the tribe, particularly *Thelypodium*. The evidence supports the conclusion that the tribe Romanschulzieae does not deserve recognition. Such a conclusion was reached earlier by Rollins (1942b) in his treatment of *Romanschulzia*. He stated "I cannot agree with O. E. Schulz (1936) that this genus represents a separate tribe in the family. Rather it should be placed in the same tribe with *Thelypodium*."

The characters Schulz used to define the tribe Streptantheae are the diagonal or oblique receptacle, the campanulate or ± bilabiate calyx, and the undulate or twisted petals. The claim that the receptacle is horizontal in all the Cruciferae but the Streptantheae does not seem to be realistic. It is true that *Streptanthus* (sensu lato) and *Caulanthus* (sensu lato) possess certain features in the petals and the calyx that are uncommon or lacking in the other primitive Cruciferae, but these differences are not strong enough to warrant putting these genera into a tribe of their own. The relationship of *Caulanthus* and *Streptanthus* to *Thelypodium*, *Chlorocrambe*, and *Thelypodiopsis* is fairly clear even though certain species of the former two genera may seem remote when compared with some species of *Thelypodium* and *Thelypodiopsis*. There are species in *Caulanthus* and *Streptanthus* that lack some features, such as the twisted or crisped petals and the campanulate or urceolate calyx,

that were considered significant in defining the Streptantheae by Schulz. He divided the Streptantheae into two subtribes the first of which, Euklisiinae, was characterized by its entire stigmas and siliques that are flattened parallel to the septum, while the subtribe Caulanthinae was said to have bilobed stigmas and siliques flattened against the replum. We believe that these subtribes are neither useful nor are they based on accurately determined characters. In addition to *Streptanthus* and *Streptanthella*, Schulz recognized eight other genera in his subtribe Euklisiinae (Table 3). These were segregated by Greene (1904, 1906a, 1906b) from *Streptanthus* on the basis of minor differences in the flowers and siliques. It is clear that these segregates of *Streptanthus* are not worth recognition since the genus otherwise is made up of a natural assembly of species.

The genus *Guillenia* was erected by Greene (1906a) to include species with reflexed siliques that were previously placed in *Thelypodium*. The two species of *Guillenia* recognized by both Greene and Schulz are *G. cooperi* and *G. flavescens*, both of which are better accommodated in *Caulanthus*, as pointed out above. However, not only did Schulz overlook the very characteristic streptanthoid flowers of these two species, but he placed *Guillenia* in the tribe Arabideae. The first three species listed by Greene (1906b) under *Guillenia* seem to represent one polymorphic species that we refer to as *Caulanthus lasiophyllus*. This species is certainly the type of the genus because it was the first one listed by Greene who stated (1904): "In arranging the sequence of species my custom is to place those first which seem to have the clearest claim to represent a genus; and therefore these stand as its type." The unfortunate thing is that Schulz maintained *Guillenia* even after he removed its type species to a different genus (*Microsisymbrium*) which he put in a different tribe, Sisymbrieae. If *Guillenia* were to be recognized, it ought to be placed in the tribe containing *Caulanthus*. However, the evidence from the morphology and cytology of the group strongly suggests that the streptanthoid genera belong to the tribe Thelypodieae.

Perhaps the best example showing the artificiality of Schulz's system is found in *Thelypodium*. The generic limits of this genus, as recognized by the present writer, include the segregate genera *Pleurophragma* and *Stanleyella*. The two segregates cannot be maintained for reasons discussed earlier. However, Schulz placed *Pleurophragma* in the tribe Arabideae, *Stanleyella* in the Sisymbrieae, and *Thelypodium* in the Hesperideae. The characters that Schulz used to distinguish these three tribes are the accumbent versus incumbent cotyledons, open versus closed calyx, and acute versus obtuse anthers. I find it very difficult to rely on these characters alone in tribal delimitations.

It is unfortunate to find that the most comprehensive monograph of the Cruciferae is the least satisfactory with respect to the tribal classifi-

cation. The use of a single character in tribal delimitation within the Cruciferae inevitably leads to an artificial classification no matter what character is used. In my opinion, the tribes should be defined on the basis of a number of characters that do not always have to be of a discontinuous nature. The tribal disposition of a given genus should be based on association with its nearest relatives and how they all fit in that particular tribe. It is true that the genera of the Cruciferae are generally difficult to determine and that their generic boundaries can sometimes be artificial, but the tribes are by no means easier to define and their boundaries may be even more artificial.

In 1942 Erwin Janchen presented a modification of Schulz's classification on the tribal and the subtribal levels only. He recognized the tribes Stanleyeae, Romanschulzieae, and Streptantheae which we believe to constitute the single tribe Thelypodieae. He placed the genera *Thelypodium* and *Thelypodiopsis* in a subtribe of their own, Thelypodiinae, which he put under the Sisymbrieae. However, such a disposition cannot be accepted since these two genera are more related to those of the three tribes mentioned above than to the members of the Sisymbrieae.

Dvořàk (1971b) maintained *Thelypodium* in the subtribe Thelypodiinae as presented by Janchen (1942). He derived it from a questionable group with incumbent cotyledons and a basic chromosome number of x=6 and indicated that the basic chromosome number in the genus is x=24. However, this number is not found in any species of the genus. It is almost certainly based on a single count made by Snow (1959) from *Caulanthus lasiophyllus* ($2n$=48) which was listed as a species of *Thelypodium*. Our chromosome counts in the genus, as well as those made by Rollins (1966), clearly indicate that a fundamental haploid number of n=13 characterizes the genus.

Present classification. The tribe Thelypodieae, as defined in the present treatment, is made up of a natural group of ten genera, most of which occur in North America. Some of these genera are presumed to be the most primitive known members of the Cruciferae. It is generally supposed that the tribe Thelypodieae might represent a link between the rest of the family and its presumed ancestors which are thought to be something like members of the subfamily Cleomoideae-Capparaceae. However, it is beyond the scope of the present paper to speculate on how the other crucifers and their tribes are connected to the Thelypodieae. It is not deemed even advisable to draw direct "phylogenetic" lines between the various genera of the tribe.

The genera *Stanelya* and *Warea* are perhaps more related to each other than to the remainder of the tribe. However, the latter genus is morphologically somewhat isolated and does not seem to tie in with the other genera as does *Stanleya*. A clear relationship appears to be present between *Thelypodium* and *Stanleya* (Rollins, 1939). The relationship be-

tween the latter genus and *Thelypodiopsis* is not entirely clear. The flowers of *T. aurea* resemble those of *Stanleya* in their color and the shape and the orientation of their petals and sepals, but there the similarities cease. Therefore, the relationships between these two genera appear to be loose and indirect. Certain species of *Thelypodium* resemble in their flowers and inflorescences some species of *Thelypodiopsis*. This is particularly evident when *Thelypodium sagittatum* and *Thelypodiopsis elegans* are compared. In fact, the two species are sufficiently similar to each other so that the latter is often misidentified as *T. sagittatum*. However, this poses a problem with respect to the relationship between the two genera, since both species appear to be advanced in their respective genera.

The genus *Thelypodium* seems to be somewhat related to *Romanschulzia* (Rollins, 1956). Such a relationship becomes evident when species with spreading floral parts of the former genus are used in the comparison. *Romanschulzia* seems to be somewhat advanced because of its small flowers and calyptra-like calyx, but we cannot say much about the genus without having a more detailed knowledge of its individual species. *Romanschulzia apetala* is somewhat similar to species of *Macropodium* in its siliques, racemose inflorescence, and long gynophores, but the two genera are distinct in their floral morphology. *Macropodium* resembles *Thelypodium* in its flowers and inflorescences more than it does other genera of the tribe. This is particularly true if *T. laciniatum*, *T. milleflorum*, and *T. brachycarpum* are used for the comparison. Although the first species of *Thelypodium* was originally described as *Macropodium* by Hooker (1830a), it should be understood that the two genera are very different in their siliques, seeds, and pubescence and I only associate them loosely.

The relationship between *Chlorocrambe* and *Thelypodium* was clearly indicated by Payson (1923). The similarities between *C. hastata* and *T. laciniatum* and *T. milleflorum* in the inflorescence, petiolate leaves, some aspects of the flowers (excluding the petals) and the pedicels are fairly clear. The former genus also resembles the three streptanthoid genera *Streptanthus*, *Caulanthus*, and *Streptanthella* in the shape of its petals, as they have broad and obovate claws, and in the broad siliques that resemble some species of *Caulanthus*. However, *Chlorocrambe* is different from any of these three genera in its toothed petals, long and distinctly exserted stamens that are somewhat equal in length, and by its distinct gynophore. The three streptanthoid genera are very clearly related to each other. The characteristic aspect of the flowers is not shared by the other genera of the tribe.

The tribe Thelypodieae is not defined by a single character. Rather a combination of characters are utilized in its definition. The following is a brief description of the tribe: flower parts erect to spreading; petals

differentiated into claw and blade or not, crisped, chanelled, or not so; stamens exserted to included, equal in length to somewhat tetradynamous or in three pairs of different lengths; anthers sagittate at base, usually coiled after dehiscence; glandular tissue mostly low and flat, usually subtending the base of filaments; siliques usually gynophorate, terete or flattened parallel to the septum; stigmas sessile or on a distinct style, entire or bilobed; seeds winged to wingless; cotyledons accumbent to incumbent.

The number of species known in the ten genera of the Thelypodieae are distributed as follows: *Stanleya* (6 species), *Warea* (4 species), *Thelypodium* (18 species), *Macropodium* (2 species), *Chlorocrambe* (1 species), *Romanschulzia* (11 species), *Thelypodiopsis* (6 species), *Streptanthus* (approximately 30-35 species), *Caulanthus* (15 species) and *Streptanthella* (1 species).

KEY TO THE GENERA OF THE TRIBE THELYPODIEAE

A. Stamens distinctly exserted, equal in length or nearly so, filaments at least 2–4 mm. above the sepals and/or petals; siliques usually long stipitate; gynophores rarely 1–2 mm. long; stigmas usually sessile.
  B. Siliques 3–6 mm. wide; seeds winged; plants of Siberia and temperate eastern Asia ..... *Macropodium.*
  B. Siliques 1–2(3) mm. wide; seeds wingless (*Chlorocrambe* sometimes with a wing-like distal edge); North America.
    C. Sepals widely spreading to reflexed; claws and/or filaments usually pubescent or tuberculate near the base; gynophores 1–3 cm. long (less than 1 cm. in some spp. of *Warea*).
      D. Flowers yellow to creamy white; inflorescence racemose; biennials or perennials; claws broader at base than above; western United States ..... *Stanleya.*
      D. Flowers white to purple; inflorescence corymbose; annuals; claws slender throughout; southeastern United States ..... *Warea.*
    C. Sepals erect; claws and filaments glabrous; gynophores mostly less than 1 cm. long.
      E. Flowers yellow-green; petals dentate between claw and blade, claws obovate, blades narrower than claws; stigmas nearly sessile; siliques 2–3 mm. wide; Utah to Oregon, United States ..... *Chlorocrambe.*
      E. Flowers white to purple; petals entire, claws slender or somewhat broader at the base, blades as wide or wider than claws; styles present; siliques 1–1.5(2) mm. wide; widely distributed in western North America ..... *Thelypodium.*
A. Stamens included to somewhat exserted, filaments equal in length, tetradynamous, or in three pairs of different lengths, when exserted, filaments not extending more than 1–2 mm. above the sepals and/or petals; siliques subsessile or stipitate; styles present (stigmas nearly sessile in a few spp. of *Caulanthus* and *Streptanthus*).
  F. Seeds winged, wing surrounding the seed or restricted to a narrow edge at the distal end of it; siliques flattened parallel to septum.
    G. Cotyledons accumbent or nearly so; styles present; valves separating from the replum along their entire length; southwestern and western United States and northern Mexico ..... *Streptanthus.*
    G. Cotyledons incumbent; siliques attenuating into style-like beak, valves separating most of their length, indehiscent above, usually with 2–4 seeds remaining in beak portion; western United States ..... *Streptanthella.*
  F. Seeds wingless; siliques mostly terete, or if flattened, then floral parts spreading.
    H. Calyx urceolate to campanulate; petals crisped or chanelled, claws as broad or

broader than the limb, often obovate to spatulate; western United States ..... *Caulanthus.*

H. Calyx not urceolate, sepals spreading to erect; petals entire, rarely crisped (a few spp. of *Thelypodium*), claws narrower than blades.

I. Sepals usually shed as flowers open; median glandular tissue surrounding the base of paired filaments; Central America to southern Mexico .... *Romanschulzia.*

I. Sepals remaining attached and usually shed after anthesis; median glandular tissue subtending paired stamens or absent; northern Mexico and western United States.

J. Stigmas bilobed, lobes opposite the replum ..... *Thelypodiopsis.*

J. Stigmas entire.

K. Siliques subsessile on a broad gynophore; pedicels stout, strongly curved, often reflexed but sometimes erect; siliques and/or pedicels usually pubescent; stems usually hollow ..... *Caulanthus.*

K. Siliques gynophorate, or if subsessile, then gynophore narrower than the fruit width, pedicels slender or stout, straight, or very slightly curved, rarely reflexed; siliques and pedicels glabrous; stems solid ..... *Thelypodium.*

There are a few genera needing some mention because they have been either associated with or compared to *Thelypodium*. *Glaucocarpum* is clearly distinct from *Thelypodium* (Rollins, 1938a) and does not seem to resemble other genera of the tribe Thelypodieae as it is presently constituted. *Ornithocarpa* is similar to both *Thelypodium* and *Romanschulzia* in its spreading parts, coiled anthers, gynophorate siliques, and filaments that are nearly equal in length, but as suggested by Rollins (1969) the genus does not seem to be phylogenetically closely related to these primitive genera. *Ornithocarpa* resembles *Schizopetalum* in its divided petals, nectar glands, divided leaves, and compressed fruits, but they are quite different in their stigmas, fruit shape, pubescence, and orientation of floral parts. The two genera were placed by Schulz (1936) in the tribe Schizopetaleae. It is not the purpose of the present paper to find a tribal classification for *Ornithocarpa*, but we feel that it does not belong to the Thelypodieae.

Pennellia presents difficulties. We have excluded it from an association with *Thelypodium* and the other primitive genera for reasons discussed previously. Schulz (1936) placed it immediately after *Halimolobos* in the subtribe Arabidopsidinae of the tribe Sisymbrieae, and the superficial resemblance of *P. micrantha* to certain species of *Halimolobos* have been pointed out by Rollins (1943). The relationship of *P. micrantha* and *P. longifolia* to the genus *Arabis* was recognized by Asa Gray (1864). The two species were then known under *Streptanthus*, but were excluded from that genus by Gray (p. 187) who suggested that they "may probably be referred to *Arabis*." Furthermore, Rollins (1941c) pointed out the remarkable resemblance between *P. micrantha* and *A. tricornuta* in their flowers, inflorescences, and general habit. All these resemblances are not accidental. It is very likely that *Pennellia* is more readily accommodated in the Arabideae than in any other tribe.

Iodanthus has been the center of a continuous controversy in terms of its tribal disposition. Prantl (1891) placed it in the subtribe Cardamininae of the tribe Sinapeae. Robinson (1895) placed it in the Arabideae while Hayek moved it to the subtribe Hesperidinae of the tribe Alysseae. Schulz (1936) placed *Iodanthus pinnatifidus* in the tribe Matthioleae and treated another species that unquestionably belongs to *Iodanthus* (cf. Rollins, 1942a) in a separate genus, *Chaunanthus*, and placed it in the tribe Sisymbrieae. Finally, Moggi (1965) maintained *Iodanthus* in the Hesperideae, while Dvořàk (1970b) maintained it in the subtribe Cardamininae of Prantl. However, the last two authors treated *Iodanthus* as a monotypic genus since they both overlooked the latest treatment of the genus by Rollins (1942a). It is clear that there is no general agreement on the tribal disposition of the genus. The present writer has no suggestion as to where the genus should go, but it cannot be placed in the Thelypodieae since it does not appear to be related to the genera we have placed in this tribe.

Morphology

Habit. All species of *Thelypodium* are typically herbaceous. One species, *T. flexuosum*, possess a distinct caudex. The majority of them are biennial, but *T. texanum*, *T. tenue*, and *T. paysonii* are winter annuals, while *T. flexuosum* and *T. eucosmum* are perennial. Under favorable conditions the potential of being short-lived perennials is present in *T. crispum*, *T. paniculatum*, *T. repandum*, and *T. sagittatum* where lateral crowns of basal leaves may be produced a few years in a row. Each crown is like a basal rosette of a biennial plant.

Stems. The stems are simple or branched from the base in the majority of species. They are mostly branched from the base in *Thelypodium stenopetalum* and, to a lesser extent, in *T. sagittatum* subsp. *ovalifolium*, while in *T. milleflorum* and *T. rollinsii* the stems are mostly simple to the inflorescence. In all species basal branching can occur as a result of grazing or the failure of the main stem to grow normally. *Thelypodium flexuosum* almost always has basal branching from the caudex, and in *T. stenopetalum* the basal branches are decumbent or subdecumbent. In one species, *T. milleflorum*, the stems can be hollow throughout or only to the inflorescence and the main stem is slightly to moderately inflated. The majority of species have glabrous and somewhat glaucous stems, but in *T. brachycarpum*, *T. crispum*, *T. howellii*, *T. sagittatum*, and *T. laxiflorum* the stems can be glabrous or pubescent near the base within the same population or in different populations. In *T. paysonii* the stems appear to be consistently hirsute throughout most of their length. The trichomes in the genus are simple and usually spreading or retrorse.

PLATE 2. Basal leaves of species of *Thelypodium* with petiolate cauline leaves.

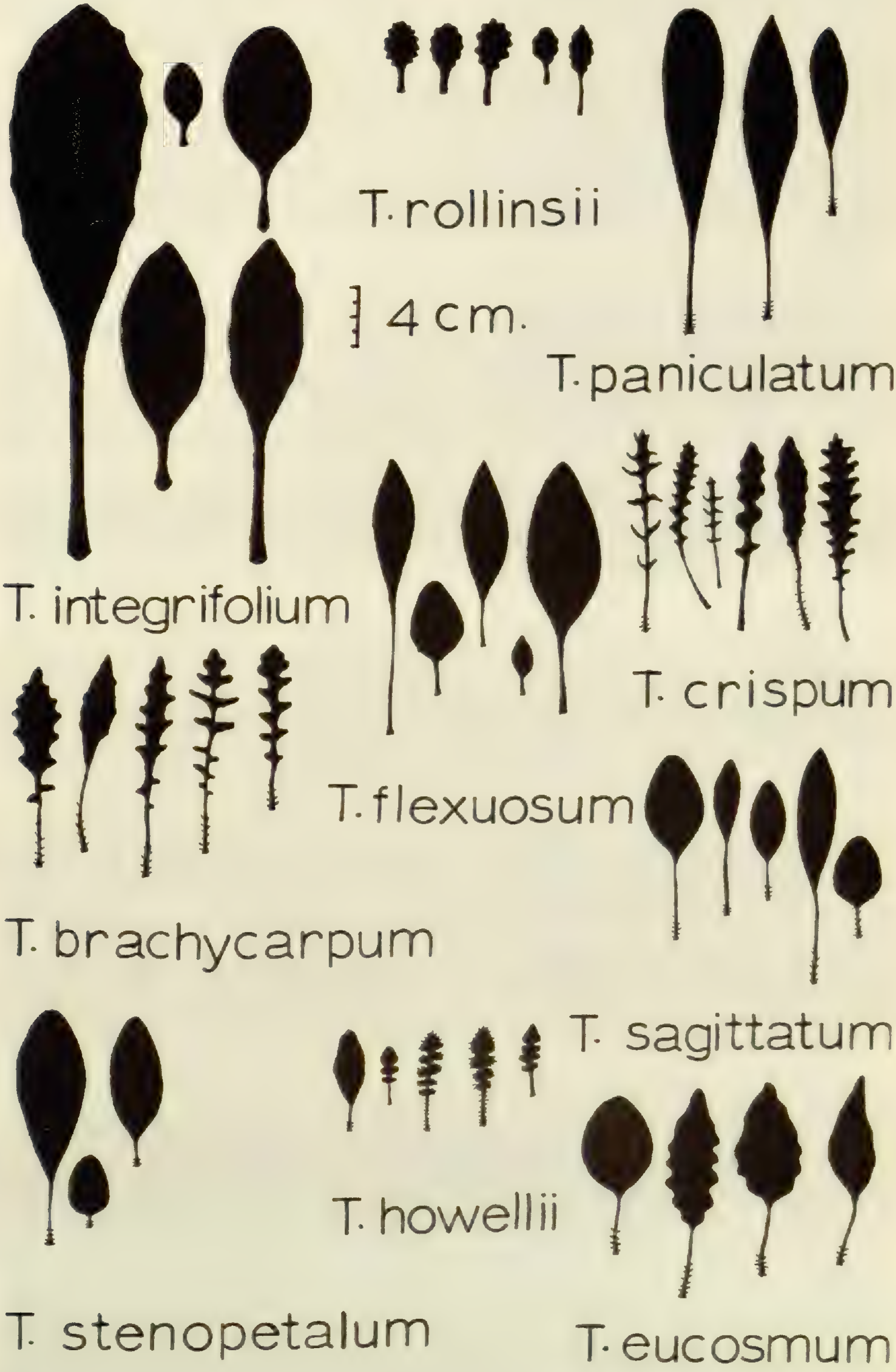


PLATE 3. Basal leaves of species of *Thelypodium* with sessile cauline leaves.

The range of stem length between the various species of *Thelypodium* can be remarkable. In *T. texanum*, *T. paysonii*, *T. repandum*, and *T. flexuosum* the stems rarely reach 7 dm. in length and in some of these and in *T. crispum* they can be as short as one decimeter. The maximum stem lengths are reached in *T. wrightii*, *T. integrifolium* subsp. *affine* and subsp. *longicarpum*, *T. milleflorum*, and *T. laxiflorum*, where they may exceed two meters in length. In the first two species I have seen plants close to three meters high. These are among the tallest known herbaceous crucifers.

Basal leaves. The basal leaves of *Thelypodium* are usually thickish (distinctly fleshy in *T. repandum*) and always petiolate. They are glabrous in all species but the six having pubescent stems. Basal leaves can be quite variable in shape, ranging from lanceolate to oblanceolate, spatulate, oblong, ovate, and obovate (Plates 2 & 3). They are typically pinnatifid or lyrate in eight species, entire in six, and variously dentate, repand, and shallowly lobed in three. In *T. howellii* they are nearly entire in subsp. *spectabilis* and usually lyrate in subsp. *howellii*. The petioles are glabrous in eight species, glabrous or pubescent in three, apparently always pubescent in *T. paysonii*, and ciliate near the base in at least six species.

The basal leaves are poorly known in most species of *Thelypodium* because they are mostly biennials where the rosette leaves wither when the flowering stems are produced. The rosettes are seldom collected independently. They are taxonomically very useful, particularly in distinguishing between certain related species, such as *T. laciniatum* and *T. milleflorum* (Plate 2) and *T. integrifolium* and *T. rollinsii* (Plate 3). Leaf margins can be quite variable within the same population in species having pinnately lobed leaves (Plate 4).

Cauline leaves. As recognized by Payson (1923), species of *Thelypodium* can be divided into three groups according to their cauline leaves. In eight species, the cauline leaves are distinctly petioled; they include *T. laciniatum*, *T. wrightii*, and their relatives. Here the cauline leaves are morphologically the same as the basal leaves but they gradually become smaller, narrower, shorter petioled, and usually less lobed toward the upper parts of the plant. In *T. integrifolium* and its five subspecies, the cauline leaves are sessile, entire, and not auriculate. Minute auricles are very rare in this species, being found in only eight plants out of more than one thousand studied. In the remaining nine species, the leaves are auriculate, sagittate, or amplexicaul. In *T. rollinsii* the leaves are appressed to the stem (Plate 17). This feature is occasionally present in *T. crispum* and *T. brachycarpum* but is not found elsewhere in the genus. The auricles can be quite variable in size within a given species, but they are characteristically small in *T. rollinsii* while in *T. sagittatum* and *T. howellii* they may exceed two centimeters in length.

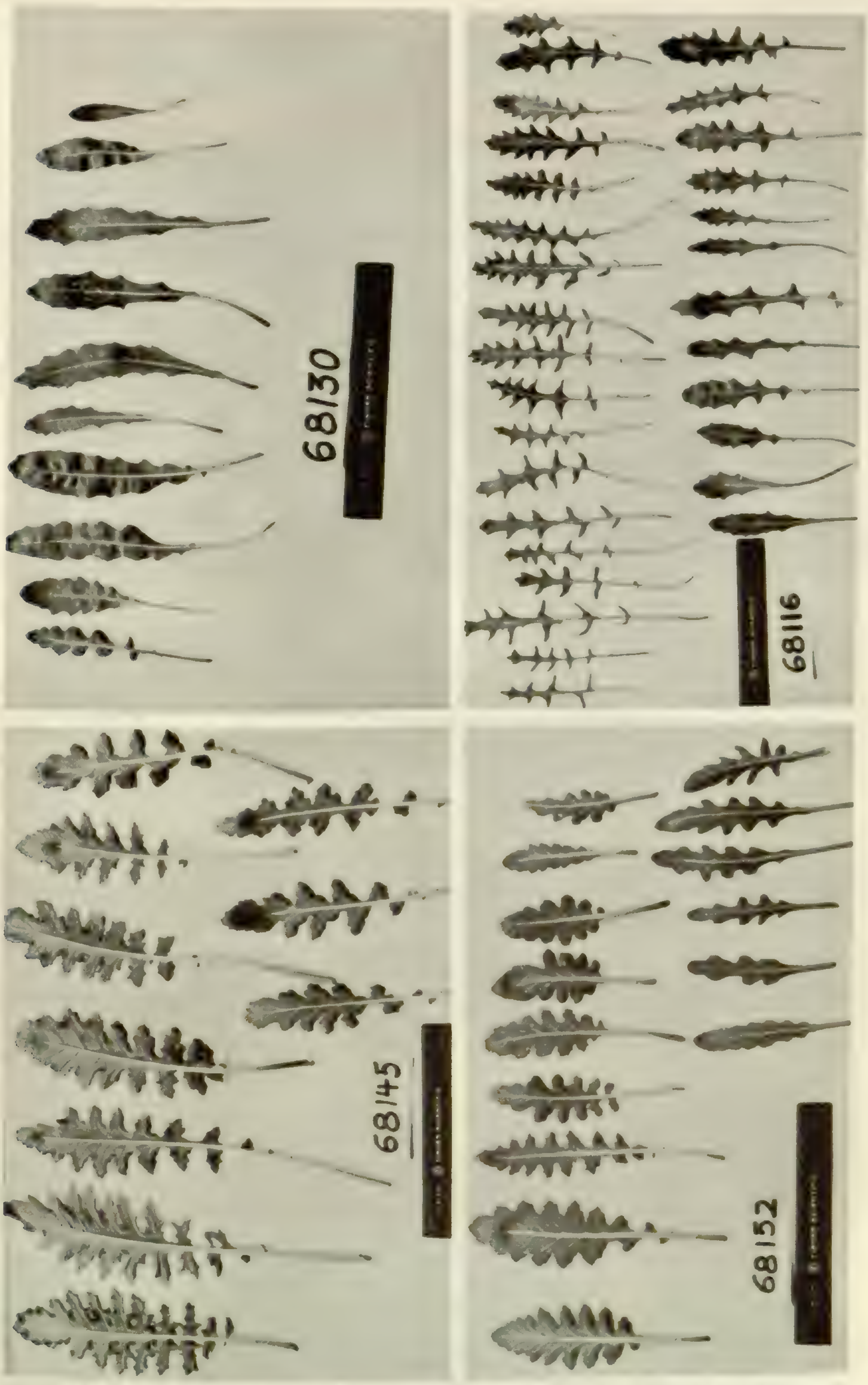


PLATE 4. Variation in basal leaves of *Thelypodium laciniatum* (68145 and 68152) and *T. crispum* (68116 and 68130).

Inflorescences. As in the majority of the Cruciferae, the inflorescence in *Thelypodium* is an ebracteate raceme or corymb terminating the main stem and the lateral branches. In six species (*T. paniculatum*, *T. flexuosum*, *T. laxiflorum*, *T. paysonii*, *T. rollinsii*, and *T. integrifolium*) the inflorescence is typically corymbose, elongating in fruit in the first four species but usually not so in *T. rollinsii*. The inflorescence of *T. integrifolium* may or may not elongate in fruit and it is a short raceme or it may be nearly corymbose in subsp. *gracilipes*. Eight species have a typical raceme and in five of these (*T. laciniatum*, *T. milleflorum*, *T. crispum*, *T. brachycarpum*, and *T. eucosmum*) it is densely flowered. However, lax inflorescences are occasionally found in the last three species mentioned. The inflorescences of *T. laciniatum* and *T. milleflorum* may reach a length of slightly more than one meter, but in the majority of species it is only a few centimeters long. In *T. howellii*, *T. stenopetalum*, and *T. repandum* the inflorescence is characteristically a lax raceme, while in the remaining four species it is usually corymbose to short racemose. The lowest flowers of the inflorescence may or may not arise from the axils of the uppermost cauline leaves, and this feature does not have any taxonomic value in *Thelypodium*.

Floral buds. The floral buds are oblong or ovate in the majority of species, but they are characteristically oblong-linear in *Thelypodium stenopetalum* and *T. eucosmum*. This serves as an excellent character to distinguish these two species from the rest of the genus.

Flowers. The flowers of *Thelypodium* show a substantial amount of variation in their size, color, and shape and in the orientation of the various floral parts. The largest flowers are found in *T. laciniatum*, *T. milleflorum*, and *T. howellii*, where they may reach 1.5 to 2.0 centimeters in length, while *T. repandum* is characterized by the smallest flowers, shorter than half a centimeter. Flower color ranges from white to dark purple but not yellow. It can be uniform in a given species or variable within the same population. The color in *T. eucosmum* is dark or red purple, while in *T. milleflorum* and *T. brachycarpum* it is always white. Various shades from white to purple are known in *T. laciniatum*, *T. sagittatum*, *T. integrifolium*, and *T. rollinsii* and these can be found within the same population or between populations. The remaining species of the genus are predominantly white or lavender-flowered.

On the basis of orientation of the floral parts to each other, two types of flowers can be recognized within *Thelypodium*. The first type, present in the majority of species, is characterized by having erect sepals, petals, and stamens. These parts can be erect throughout their length or along their lower half. The stamens are usually spreading or ascending above when they are exserted and clearly erect when included. This type characterizes species such as *T. laciniatum*, *T. eucosmum*, *T. rollinsii*, *T. stenopetalum*, *T. sagittatum* and their relatives (Plate 5). The second type, where the sepals, petals, and stamens are spreading from their bases, is

present in *T. wrightii*, *T. texanum*, *T. repandum*, *T. tenue*, and less clearly so in *T. paysonii* (Plate 5). The sepals of *T. wrightii* are sometimes reflexed, a feature not found elsewhere in the genus. The stamens, on the other hand, are usually spreading to an angle of 45 degrees and

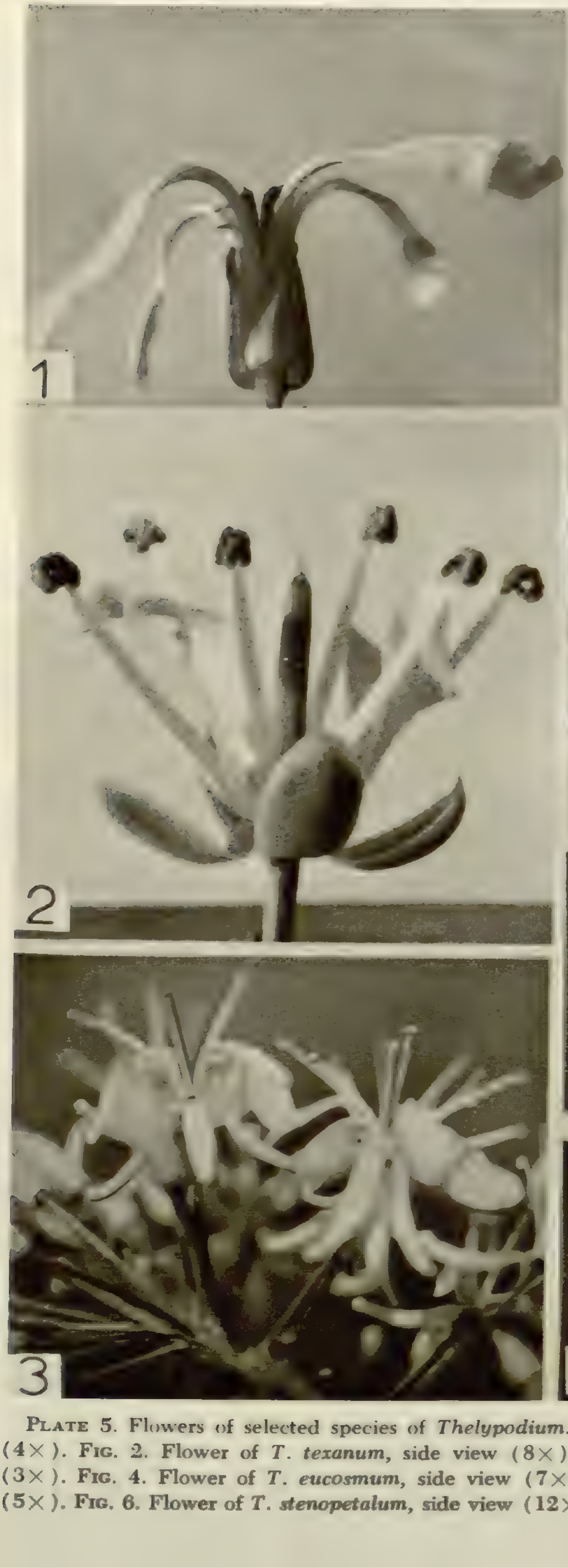


PLATE 5. Flowers of selected species of *Thelypodium*. FIG. 1. Flower of *T. sagittatum*, side view (4×). FIG. 2. Flower of *T. texanum*, side view (8×). FIG. 3. Flowers of *T. wrightii*, side view (3×). FIG. 4. Flower of *T. eucosmum*, side view (7×). FIG. 5. Flower of *T. texanum*, top view (5×). FIG. 6. Flower of *T. stenopetalum*, side view (12×).

equally spaced between each other so that the single and the paired stamens do not stand out since they are all equal in length or nearly so. However, the single stamens are always opposite to the outer pair of sepals, and this serves to distinguish between the two types of stamens. The paired stamens of *T. wrightii* are sometimes closer to each other than to the single stamens. In *T. laxiflorum*, a close relative of *T. wrightii*, the sepals are ascending to spreading or erect, and the petals and stamens are erect at the base (Plate 22).

Sepals. The sepals are glabrous in all species of *Thelypodium*. The variation in their color and orientation is discussed above. One feature worth mentioning is that the sepals are somewhat saccate and unequal at the base in *T. sagittatum*, *T. paniculatum*, *T. howellii*, *T. flexuosum*, and less clearly so in some other species. In *T. laciniatum*. *T. milleflorum*, *T. eucosmum*, and less clearly in *T. crispum* and *T. brachycarpum* they are saccate and nearly equal at the base, while in those species where they are spreading or reflexed the sepals are nonsaccate and equal at the base.

Petals. The petals of *Thelypodium* show a wide range of variation in size, shape, orientation, and color (Plate 6) and therefore are often useful taxonomically. They may be differentiated into a distinct claw and blade in species such as *T. laciniatum*, *T. milleflorum*, *T. crispum*, *T. brachycarpum*, *T. eucosmum*, and *T. paysonii*, or the blades are attenuated to a narrow claw-like base, as in most of the remaining species. The blades are narrowly linear in *T. stenopetalum* and linear in *T. crispum*, *T. brachycarpum*, and *T. laciniatum*. The broadest, often obovate, petals are found in *T. paniculatum* and, to a lesser extent, in *T. flexuosum*. The petals may be crisped throughout most of their blade, as in *T. crispum*, and *T. brachycarpum*, or between the claw and blade, as in *T. stenopetalum* and *T. howellii*. The petals in most of the remaining species are usually not crisped. The claws in *T. laciniatum* and *T. milleflorum* are most often thicker than the thin blades, while in *T. paysonii* they are covered with short gland-like trichomes near their bases. These features of the claws are very useful in distinguishing these particular species of *Thelypodium* from the rest.

Filaments. The filaments of *Thelypodium* show two interesting features. First, they are spreading in species such as *T. texanum*, *T. tenue*, *T. wrightii*, *T. paysonii*, and *T. repandum*, while they are erect below in the majority of the remaining species. The orientation of the stamens (erect versus spreading) served as an excellent character to distinguish between the closely related species *T. wrightii* and *T. laxiflorum* (Plate 22). Second, in the majority of species with exserted anthers the filaments are equal in length or nearly so. This is particularly true of *T. laciniatum*, *T. milleflorum*, *T. eucosmum*, *T. texanum*, and *T. wrightii*. On the other hand, in *T. laxiflorum*, *T. stenopetalum*, *T. sagittatum*, *T. paniculatum*, and *T. flexuosum* the filaments are tetradynamous. The re-

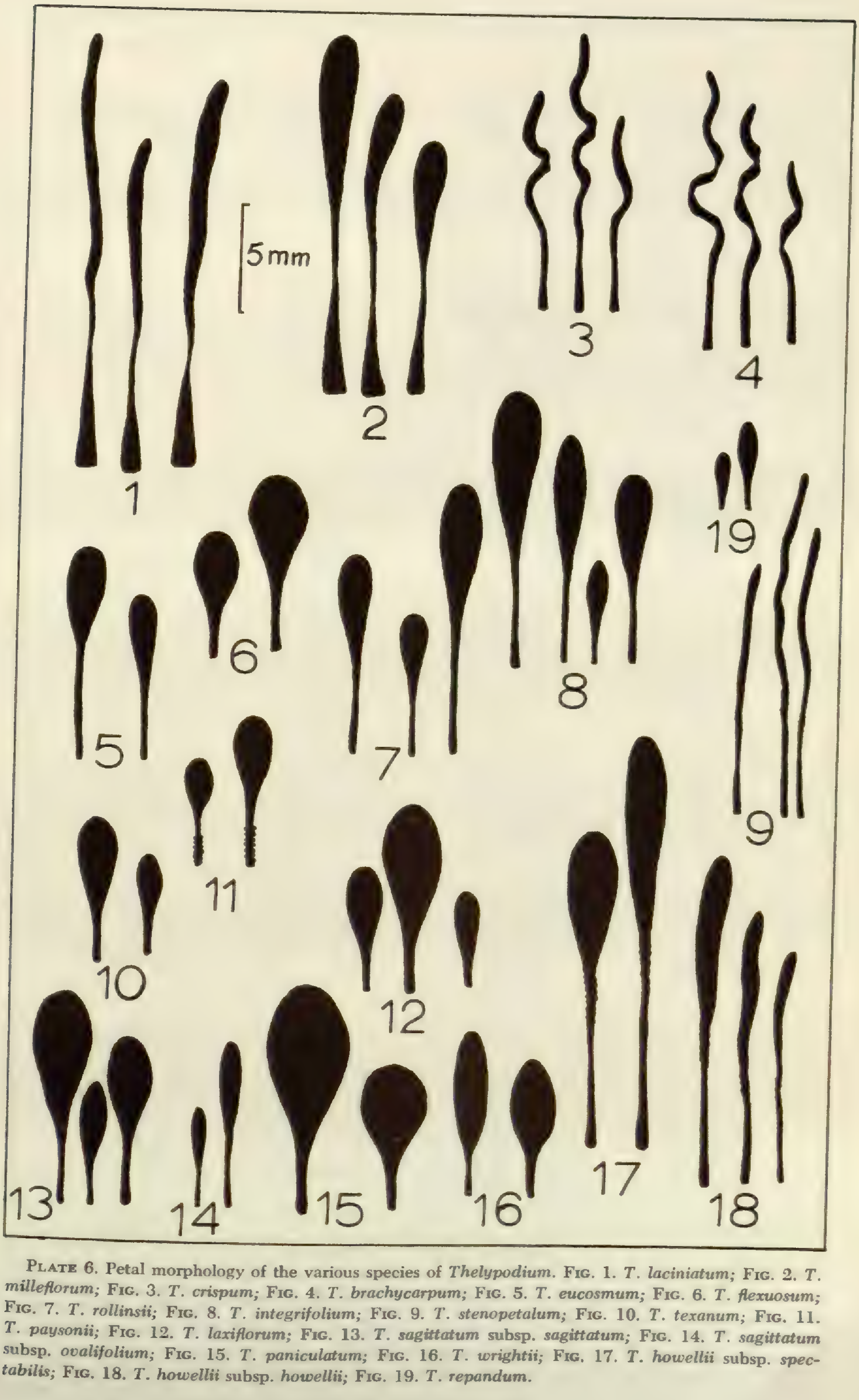


PLATE 6. Petal morphology of the various species of *Thelypodium*. FIG. 1. *T. laciniatum*; FIG. 2. *T. milleflorum*; FIG. 3. *T. crispum*; FIG. 4. *T. brachycarpum*; FIG. 5. *T. eucosmum*; FIG. 6. *T. flexuosum*; FIG. 7. *T. rollinsii*; FIG. 8. *T. integrifolium*; FIG. 9. *T. stenopetalum*; FIG. 10. *T. texanum*; FIG. 11. *T. paysonii*; FIG. 12. *T. laxiflorum*; FIG. 13. *T. sagittatum* subsp. *sagittatum*; FIG. 14. *T. sagittatum* subsp. *ovalifolium*; FIG. 15. *T. paniculatum*; FIG. 16. *T. wrightii*; FIG. 17. *T. howellii* subsp. *spectabilis*; FIG. 18. *T. howellii* subsp. *howellii*; FIG. 19. *T. repandum*.

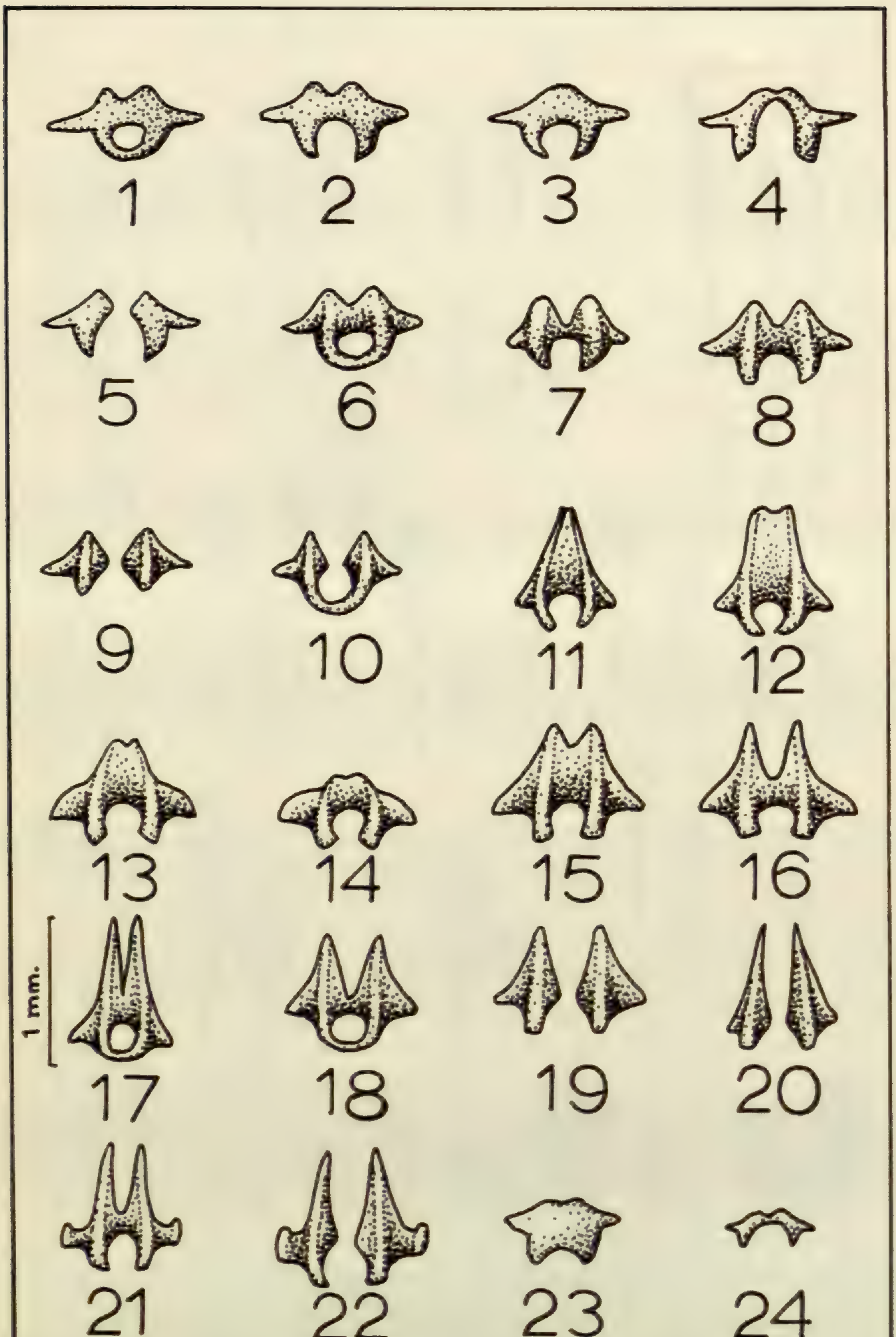


PLATE 7. Variation in nectar glands of *Thelypodium integrifolium*. FIGS. 11–18 illustrate forms most common in ssp. *affine* and ssp. *longicarpum;* FIGS. 6–10 are common forms in ssp. *gracilipes* and ssp. *complanatum;* FIGS. 1–24 may be found within ssp. *integrifolium*.

maining species of the genus are intermediate between the two species groups. One feature of *T. paysonii*, not found anywhere else among the primitive Cruciferae except in the genera *Stanleya* and *Warea*, is the presence of short trichomes on the lower parts of the filaments and claws.

Anthers. The anthers in all species of *Thelypodium* are introrse, basifixed, and sagittate at the base. In a few species they are apiculate while in the rest they are not. No characters of taxonomic value are offered by the anthers. Where they are long and exserted, the anthers become strongly coiled after dehiscence, a feature common in the most primitive genera of the tribe Thelypodieae. On the other hand, the anthers, in the species where they are included, remain straight or slightly curved after dehiscence.

Glandular tissue. The nectar glands of the family Cruciferae received considerable attention from a number of investigators around the turn of the 20th century, or earlier, starting with the work of Hildebrand (1879). Bayer (1905) was the first to elaborate a classification system for the family based primarily on the characteristics of the nectar glands. In connection with *Thelypodium*, Payson (1923) relied heavily on them to distinguish three out of four "species" related to *T. integrifolium*. As in other aspects of the plant, nectar glands are fairly constant in certain species and extremely variable in others. Similar observations were made by Snogerup (1967) in the genus *Erysimum*. Two basic types of glandular tissues are present in *Thelypodium*. The first is characterized by the presence of lateral glands only, which are developed more above the base of single stamens than beneath. They are usually flat and low, but can be tooth-like in most populations of *T. integrifolium*. Other species that have lateral glands only are: *T. crispum*, *T. brachycarpum*, *T. flexuosum*, and most populations of *T. howellii* subsp. *howellii* and *T. sagittatum* subsp. *sagittatum*. The second type is a continuous disc subtending the bases of paired filaments and surrounding or subtending the bases of single filaments. This type is characteristic of the remaining taxa of the genus.

Thelypodium integrifolium is the most variable species of the genus in its nectar glands. As shown in Plate 7, the glands vary considerably in terms of being flat or tooth-like and whether the "teeth" are united or separated. However, it is not possible to distinguish between the various subspecies of *T. integrifolium* on the basis of their glands in the way that Payson did (1923).

Fruiting pedicels. Characters of the fruiting pedicels, such as length, orientation, stoutness, and the nature of their bases, are very useful in distinguishing between the various species of *Thelypodium*. The shortest pedicels in the genus are found in *T. brachycarpum*, where they hardly exceed 1–2 mm. in length, while in *T. tenue* they can be as long as 2–3.5 cm. Pedicel orientation is usually a conservative feature in most species, but it may vary from divaricately ascending to divaricate or variously

reflexed in species such as *T. wrightii, T. laxiflorum,* and, to a lesser extent, *T. integrifolium* subsp. *longicarpum.* Pedicels are horizontally attached to the rachis in the majority of species, but they are erect or nearly so and usually appressed to the rachis in *T. crispum,* while in *T. howellii* they are mostly ascending. In most species they are straight or slightly curved, but in *T. milleflorum* they are strongly curved up, usually with an erect tip. Pedicel length may show considerable variation within a given species. This is particularly true in *T. sagittatum, T. laciniatum,* and *T. integrifolium.* In most species, the lowest pedicels of the infructescence are longer than the uppermost ones.

Siliques. As stated by Rollins (1941c), the siliques are extremely valuable in the identification of genera and species in the Cruciferae. They are very useful in distinguishing species or species groups within *Thelypodium* and, more important, in separating this genus from related genera. Payson (1923) depended heavily on the cellular pattern of the septum in defining the generic limits of *Thelypodium.* He excluded *T. wrightii* from the genus and accepted its disposition in a genus of its own, *Stanleyella* Rydberg, because it was said to lack the central band of elongated cells and the lateral tortuose cells that characterize the septum of *Thelypodium.* The other characters on which *Stanleyella* was based were evaluated in the section on generic relationships. These alleged differences in the septum are not consistent. In my opinion, the cellular patterns of the septum have a very limited value, if any, at the various taxonomic levels within the tribe Thelypodieae. Dvořàk (1970a) used them in distinguishing species groups with *Malcolmia* and as a criterion of evolutionary relationships within the Cruciferae (Dvořàk, 1971a), but Stork (1972) questioned their value in *Malcolmia,* since she found significant variation within a given taxon.

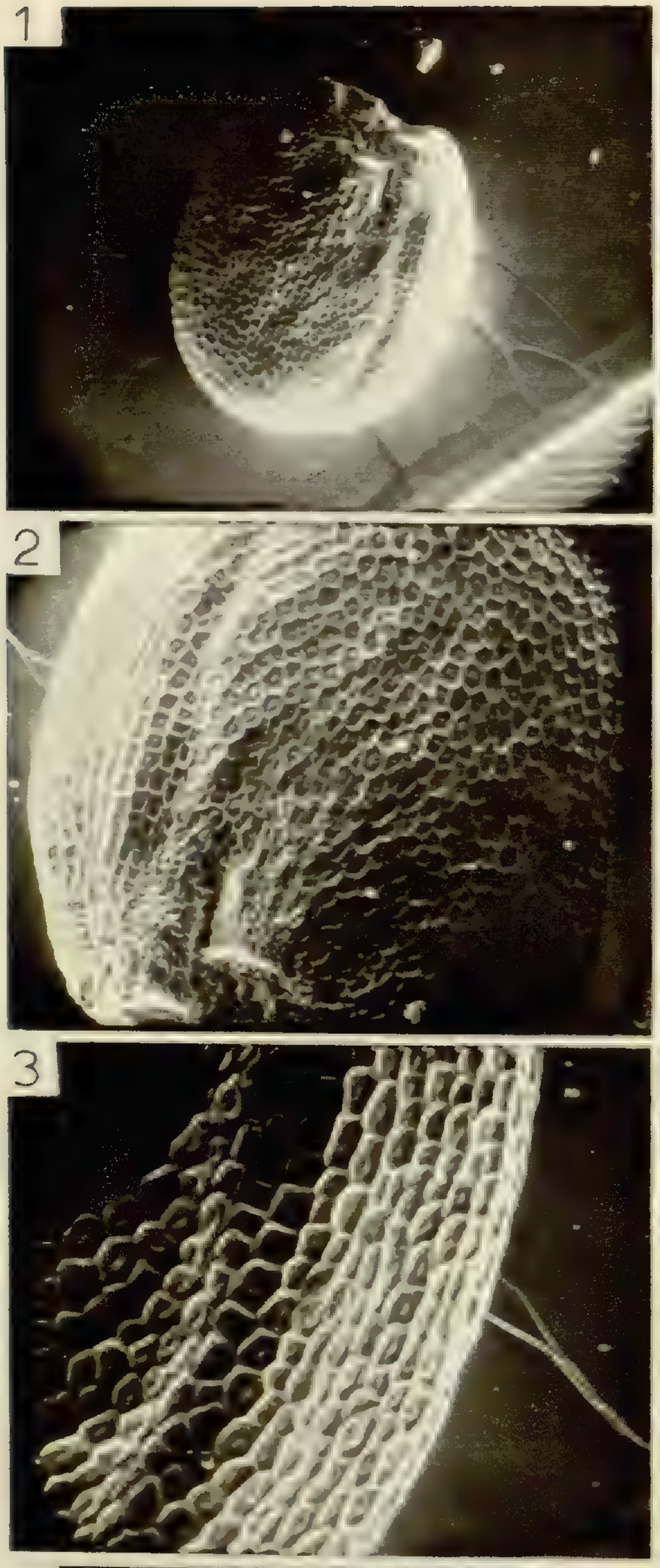
With the exception of *Thelypodium paysonii,* the siliques are torulose throughout the genus. In *T. laciniatum, T. milleflorum, T. wrightii, T. repandum, T. texanum,* and *T. paysonii* they are somewhat flattened parallel to the septum, while in the remaining species they are clearly terete. Mature fruits of *T. tenue* are not known. Silique length has a very limited taxonomic value in this genus. A maximum length (10–12 cm.) is reached in *T. laciniatum* and *T. milleflorum* and minimum lengths (0.6–1.5 cm.) are found in *T. crispum, T. brachycarpum,* and *T. flexuosum.* Silique width is only useful in distinguishing between the two closely related species *T. paniculatum* and *T. sagittatum.*

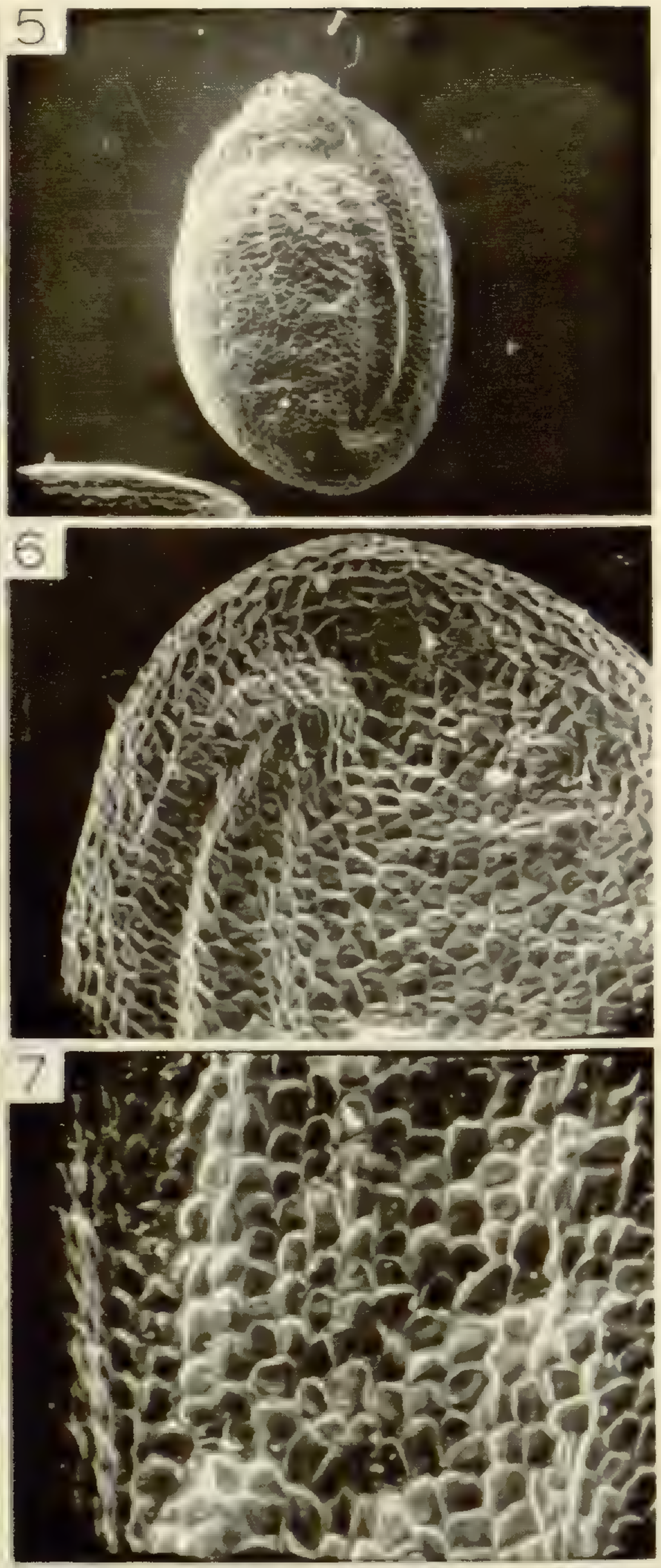
Styles and stigmas. The style in most species of *Thelypodium* is slender and usually narrows from the base to the stigma. In some species, such as *T. wrightii, T. laxiflorum, T. repandum,* and occasionally in *T. laciniatum* and *T. milleflorum* the style is subclavate. The stigmas are entire and almost always equal to or smaller than the diameter of the style. Although these features of the style and stigma have little or no

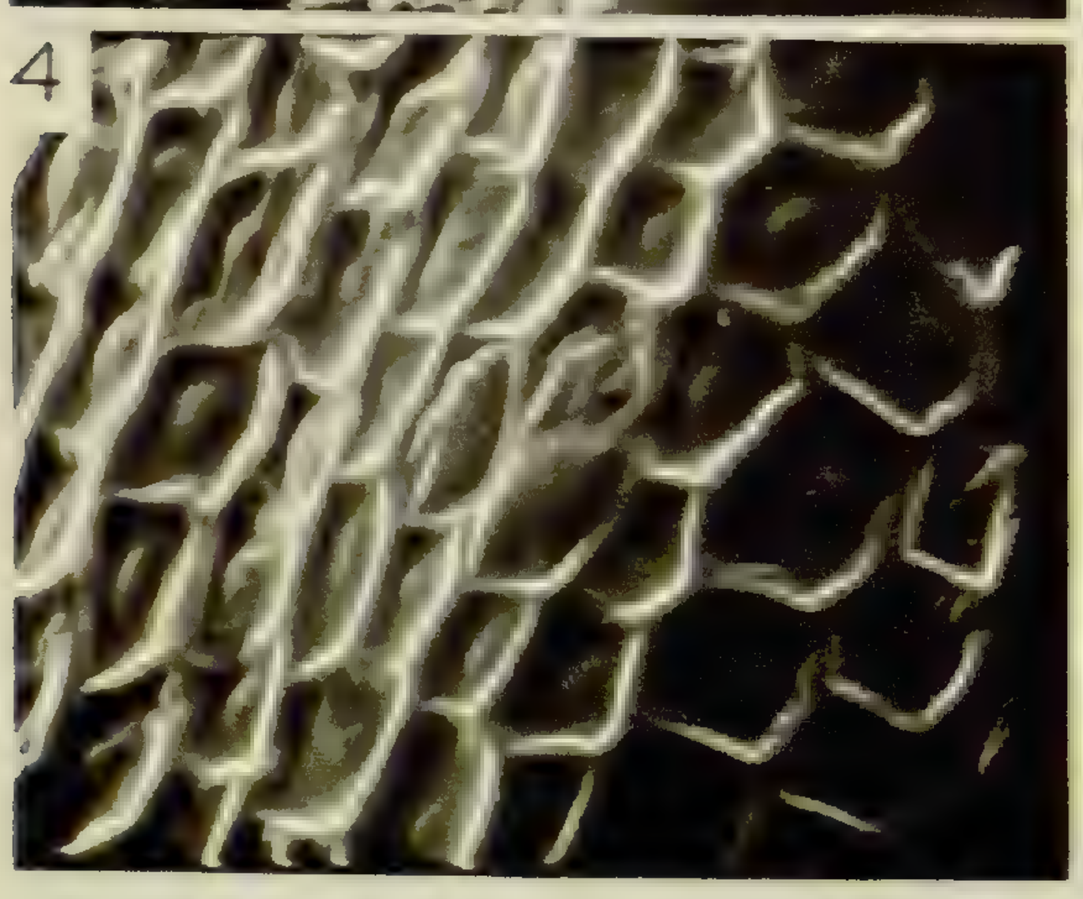
significance on the species level, they are most useful in distinguishing between *Thelypodium* and the related genus *Thelypodiopsis* (Plate 1).

Gynophore. All species of *Thelypodium* have a distinct gynophore that is always narrower than the fruit itself. It can be as short as ½ mm. or as long as 8.5 mm. In *T. paniculatum*, *T. flexuosum*, *T. laxiflorum*, *T. texanum*, and *T. repandum* the gynophore hardly excedes one millimeter in length, while in *T. milleflorum*, *T. laciniatum*, and *T. eucosmum* it is usually longer than 2 mm. Gynophore length is usually quite variable within the same population. This is particularly true in species where it is most frequently longer than 1 mm. (Plate 8).

PLATE 8. Variation in gynophore length of *Thelypodium laciniatum*. Scale in millimeters.







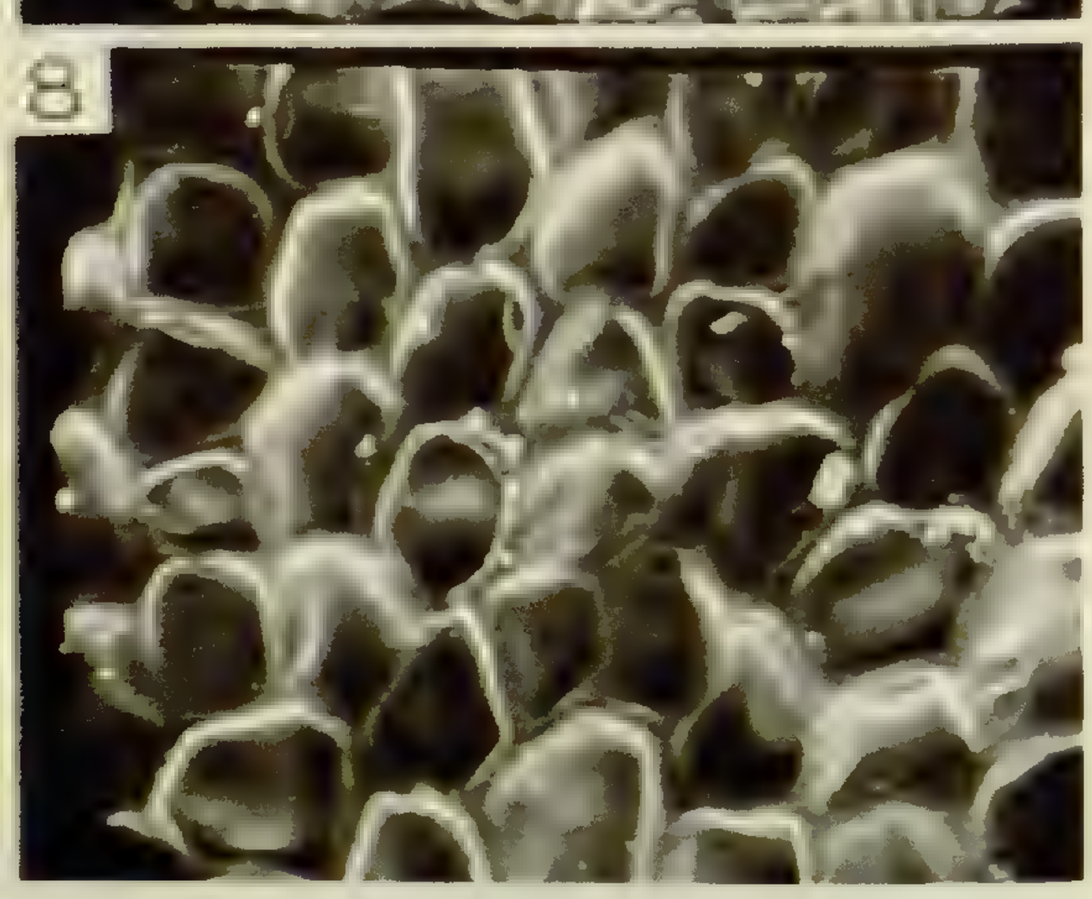


PLATE 9. SEM photomicrographs of seeds of *Thelypodium* and *Stanleya*. FIGS. 1–4. *T. texanum*, Barclay 713; FIGS. 5–6. *T. laciniatum*, Al-Shehbaz 6922; FIGS. 7–8. *Stanleya pinnata*, Al-Shehbaz 6986. Magnifications: 1. 25×; 2. 49×; 3. 98×; 4. 245 ×; 5. 37×; 6. 98×; 7. 100 ×; 8. 250×.

Seeds. The seeds in all species of *Thelypodium* are wingless, uniseriate, faintly reticulate, non-mucilaginous, oblong to ovate, and brownish in color. The cotyledons are obliquely accumbent to obliquely incumbent. However, one occasionally finds accumbent or incumbent cotyledons in species that have flattened or terete siliques respectively. The percentages of these two cotyledonary positions in a given seed sample range between 1 to 10% in the majority of the species.

As stated by Payson (1923), seed morphology does not contribute much to the taxonomy of *Thelypodium*. The differences in seed dimensions, if present, are so slight as to be insignificant. Seeds of *T. paniculatum* and *T. brachycarpum* are decidedly plump, while their respective relatives, *T. sagittatum* and *T. crispum*, have somewhat flattened seeds.

Seed sculpture is uniform throughout *Thelypodium*. According to the terminology used by Murley (1951), the seed surface is minutely reticulate. Seeds of 16 of the 18 species of the genus were examined under the scanning electron microscope. The sculpture (Plate 9) is mostly made up of hexagonal or pentagonal units that are not arranged in any particular fashion. However, those units above the radicle are tetragonal and arranged in lines parallel to its long axis. Seeds of *Thelypodium* are fairly similar to those of the related genus *Stanleya*, the main differences being the presence of pustulae (one in the center of each unit) and the angulate nature of the units in the former genus, and their absence from the single species studied of the latter (Plate 9).

Distribution, Ecology, and Economic Importance

Distribution. The genus *Thelypodium* occurs primarily in the western part of the United States. Two of its species, *T. laciniatum* and *T. milleflorum*, are also present in Canada, but these are known from old collections made from southern British Columbia (Henry, 1915). One species, *T. paysonii*, is endemic to northern Mexico and appears to be restricted to southern Coahuila and adjacent Durango. However, very few collections of this species were available for study and more are needed before a clear picture of its distribution can be presented. The only species found in both Mexico and the United States is *T. wrightii*.

Within the United States, *Thelypodium* is distributed in an area defined on the east by an imaginary line extending from central North Dakota southward through western South Dakota, western Nebraska, eastern Colorado, northwestern Oklahoma, eastern New Mexico, and southwestern Texas. On the west, the area is defined by the eastern slopes of the Cascade Mountains in Washington and Oregon and the eastern slopes of the Sierra Nevada Mountains and San Bernardino Mountains in California. Seventeen of the twenty-five taxa recognized in the present treatment occur in the Great Basin, with the majority of them (twelve) found in Nevada and Utah. The most widely distributed species are *T.*

integrifolium, *T. sagittatum*, *T. milleflorum*, and *T. laciniatum* (Maps 1, 3, and 4). The most restricted species are known from one or very few counties. *Thelypodium repandum* is known only from Custer County, Idaho, while *T. stenopetalum* is endemic to Bear Valley in San Bernardino County, California. One remarkable species, *T. tenue*, is known only from the type collection made in Presidio County, Texas. Finally, three species, *T. eucosmum*, *T. texanum*, and *T. rollinsii*, are known from very few counties in Oregon, Texas, and Utah respectively. *Thelypodium texanum* occurs in a number of localities in Brewster County, but has not been collected, to my knowledge, from the neighboring areas of northern Mexico.

Altitudinal ranges. There is a wide range of variation in the altitudinal limits reached by the various species of *Thelypodium*. Species that are narrow endemics show very little variation in altitude, but widely distributed species, such as *T. laciniatum*, *T. integrifolium*, *T. wrightii*, *T. milleflorum*, and *T. crispum*, have maximum and minimum limits that differ by 6,000 feet or more. The lowest elevation (100 to 500 feet) is reached by *T. laciniatum* and *T. milleflorum*, while *T. laxiflorum*, *T. sagittatum*, and *T. paniculatum* are known to grow at elevations of ca. 9,000 feet. Certain populations of *T. crispum* have reached the highest limits for the genus. A few plants have been collected from altitudes as high as 10,500 feet in the Virginia Lakes region of California (*M. & L. Smith* 335, CAS).

Habitats. Species of *Thelypodium* are found in various types of habitats with alkaline to non-alkaline soils that are wet or dry, sandy, loamy, or clay-like; limestones, sandstones, or serpentine rock and talus; in open meadows, rocky slopes, sunny flats or slopes, shaded canyons, streamsides, and sand dunes (Table 4).

Some of the widely distributed species, such as *T. integrifolium* and *T. laciniatum*, occupy a variety of habitats, while the endemic species have a rather narrow habitat preference. For example, *T. repandum* prefers the loose and decomposing shale on the steep canyons of the Salmon River in Custer County, Idaho. The soil in such a habitat is unstable and dries out quickly. Plants of this species are probably adapted to such conditions by having a rather deep root system, short stems, and distinctly fleshy leaves. At least eight species are known to grow in alkaline meadows or flats and some of them, *T. crispum*, *T. brachycarpum*, and *T. flexuosum*, can tolerate strongly alkaline soils in which very few other plants are found. Plants of *T. flexuosum* have slender and weak stems that receive their support by being twisted between the branches of desert shrubs under which they grow. Some of these shrubs are the greasewood, *Sarcobatus vermiculatus*, sagebrush, *Artemisia tridentata*, *Atriplex* spp., and *Chrysothamnus* spp. Being long-lived perennials, plants of *T. flexuosum* are well-established in such habitats. Unlike other species of *Thelypodium*, the stems are very few-leaved in this species and the

TABLE 4. SPECIES OF THELYPODIUM, THEIR HABITATS AND THE ASSOCIATIONS IN WHICH THEY GROW

	alkaline meadows or flats	wet sedge meadows	decomposing shale banks	rocky slopes & crevices of cliffs	sand dunes or sandy soils	mineralized soils of hot springs	shady slopes of canyons	barren hillsides	serpentine rock or talus	limestone ledges	streamsides, river banks, creek beds	strongly alkaline desert flats	desert shrub communities	pinyon-juniper association, junipers, oak-woodland
T. laciniatum				x			x		x	x				
T. milleflorum					x								x	
T. crispum	x					x						x		
T. brachycarpum	x											x		
T. eucosmum							x				x			x
T. rollinsii	x													
T. integrifolium	x					x		x		x	x	x	x	
T. stenopetalum	x													
T. howellii	x												x	
T. sagittatum	x										x			
T. paniculatum		x									x			
T. flexuosum												x	x	
T. wrightii				x		x					x			x
T. laxiflorum				x		x					x			x
T. repandum			x											
T. texanum							x				x			

major photosynthetic part is the basal leaves that are shed at the end of the growing season. In the remaining species of the genus, basal leaves are shed as the stems grow and the cauline leaves are formed. *Thelypodium sagittatum* was said to grow in association with *Sarcobatus* (Holmgren, 1972), but it is likely that the species meant was *T. flexuosum*.

The only species of *Thelypodium* clearly adapted to wet conditions is *T. paniculatum*. It grows in wet sedge meadows where the water level may cover the basal portion of the plant. Its closest relative, *T. sagittatum*, is also found in meadows, but it usually prefers much drier sites and alkaline soil.

With the exception of a few species, *Thelypodium* is adapted to somewhat arid or semiarid conditions. Seven species are listed in Table 4 as growing near streamsides, river banks, and creek beds, but otherwise most of them occur in dry places. *Thelypodium milleflorum* and *T. flexuosum* are the only two species that appear to tolerate the high degrees of aridity of open deserts, while *T. crispum*, and, to a lesser extent, *T. in-*

tegrifolium can withstand the highly mineralized soils adjacent to hot springs. The majority of species grow in open areas that are directly exposed to sunlight, but *T. wrightii*, *T. laxiflorum*, *T. eucosmum*, and *T. laciniatum* grow in shady as well as open habitats.

Economic importance. Very few reports are available on the economic value(s) of the various species of *Thelypodium*. Vasey and Rose (1890) published the following field note made by Edward Palmer on the plants of *T. integrifolium* subsp. *affine:* "The leaves are cooked and eaten by the Indians. Cattle do not seem to feed on this." A similar note was made by Elzada Clover on herbarium sheets (*Clover 5113*, DS & MICH) that the plants of *T. integrifolium* subsp. *longicarpum* are "used as spinach by Supais." Hermann (1966) mentioned that *T. laciniatum* "appears to be valuable for sheep early in the season where it grows in sufficient quantity" and that *T. integrifolium* "appears to be of some forage value under certain conditions." From my field experience with most species of *Thelypodium* growing in open ranches where cattle were present, the plants were mostly healthy looking and relatively few of them were eaten. It is likely that the plants are avoided by cattle and that occasional eating might be accidental. No other usages or values are known and it is clear that the genus has no economic significance.

Reproductive Biology

Flowering. In the annual species of *Thelypodium*, such as *T. texanum*, *T. tenue*, and *T. paysonii*, the life cycle of the plant appears to be directly related to the availability of rain, and flowering probably takes place a few weeks after seed germination. Photoperiodism does not appear to be a crucial factor in the flowering of *T. texanum*, since the plants flowered in growth chambers with 8, 12, and 16 hours of daily light periods.

As for the biennial and perennial plants, photoperiodism alone has no effect. The main requirement to induce flowering probably is subjection to cold. The fifteen biennial and perennial species of *Thelypodium* seem to have an obligate cold requirement, since the untreated rosettes failed to flower and some of them remained in such a stage from one to three years. Biennials with an obligate cold requirement grown under non-inductive conditions, in which they remain growing vegetatively, can be induced to flower by treating them with gibberellic acid (GA_3) (Lang, 1957, 1965; Michniewicz & Lang, 1962). This might be a useful approach to follow in order to study the flowering and the breeding systems of *Thelypodium*. The GA_3 solution used was prepared as follows: 25 mg. of gibberellic acid (Eastman Organic Chemicals) dissolved in 500 ml. of 0.05% tween 20 (Fisher Scientific) as a wetting agent. The resulting solution (concentration 50 μg/ml.) was applied dropwise to the growing center of the rosette, which received 2 drops (approximately 5 μg of GA_3) every other day.

The response of the various species of *Thelypodium* to the gibberellin treatment was different. Three species, *T. brachycarpum*, *T. paniculatum*, and *T. howellii*, showed no signs of bolting and/or flowering and remained in the rosette stage after a period of gibberellin treatment extending nearly five months. The best, and by far the most consistent, response to this treatment was shown by *T. stenopetalum*. Five to fourteen applications were sufficient for bolting and three to six additional ones were necessary to induce flowering. Plants of *T. paysonii* and *T. tenue* were not available for such a treatment. The other eleven species that flowered showed no signs of consistency in terms of the number of applications needed for bolting and flowering. In certain species the response was fast in some rosettes and much slower in others. It is beyond the scope of this study to go into the details of this treatment, but it is clear that it is a valuable approach to obtain flowering for the study of breeding systems in some species of *Thelypodium*.

Pollination. Almost all species of *Thelypodium* have showy flowers that range in color from white to dark purple. They often produce nectar and are usually grouped in dense inflorescences, undoubtedly contributing to the attraction of insects for pollination. By far the most common visitors are two types of bees belonging to the genera *Bombus* (Bumblebee) and *Apis* (Honey-bee, *A. millefera*) of the family Bombidae. Carpenter bees of the genus *Xylocopa* (family Xylocopidae) were fairly common on plants of *T. integrifolium* in Arizona, Utah, and Nevada. A few unidentified species of bees also were found. One species of butterfly of the family Lycinidae was seen, but only a few times, on plants of *T. rollinsii*. Some members of the butterfly genus *Pieris* (probably *P. sisymbrii*) of the family Pieridae were fairly common visitors to the flowers of *T. rollinsii*, *T. integrifolium*, *T. laciniatum*, and *T. wrightii*.

Breeding systems. The evidence available from all 13 species that flowered in the greenhouse was that autogamy did not occur in most species. Representatives of eight species are clearly self-compatible. They are: *Thelypodium integrifolium* (subsp. *affine*, subsp. *integrifolium*, and subsp. *longicarpum* were tested), *T. laxiflorum*, *T. milleflorum*, *T. repandum*, *T. rollinsii*, *T. stenopetalum*, *T. texanum*, and *T. wrightii* subsp. *wrightii*. Plants of two of the remaining five species, *T. sagittatum* and *T. flexuosum*, showed that they are probably self-incompatible. However, the evidence was not conclusive. Whether these findings will hold in other populations of the species so far investigated in a preliminary way remains to be determined. It should be kept in mind that both self-compatibility and self-incompatibility may be present in the same taxon (Rollins, 1963a; Lloyd, 1965).

The flowers of *Thelypodium* possess certain features that appear to reduce the chances of selfing. In the species with distinctly exserted anthers, the stigmatic surface is always below the anthers in the recently opened flower. As the anthers dehisce, they become distinctly coiled and

the filaments become ascending or somewhat recurved. At the same time, the pistil elongates and the stigmatic level is raised, but almost never touches the anthers. This type of flower is characteristic of *T. laciniatum*, *T. milleflorum*, *T. eucosmum*, *T. crispum*, *T. brachycarpum*, and, to a lesser extent, *T. integrifolium* and *T. rollinsii*. In three of the five species with spreading floral parts, *T. wrightii*, *T. texanum*, and *T. repandum*, the filaments are well spread by the time the anthers start to dehisce and the pistils are at some distance from the anthers.

In some plants of *Thelypodium texanum* grown under greenhouse conditions, the styles were observed to emerge from the floral buds two to three days before the flowers opened. This is a clear case of protogyny. Unfortunately, we do not know how common protogyny is in natural populations of this species. Protogyny, protandry, and dioecy were said to be lacking in the Cruciferae (Bateman, 1955a). Dioecism occurs in three species of *Lepidium* from New Zealand (Kirk, 1899; Bateman, 1955b; Allan, 1961). Protandry is known in three species of *Streptanthus* (Kruckeberg, 1957; Rollins, 1963b). The earliest report on protogyny in the Cruciferae probably dates back to Kerner (1895), who stated that ". . . and Cruciferae exclusively protogynous." However, neither he nor Faegri and van der Pijl (1966) gave any examples. Protogyny is now well-known in *Arabis* (Rollins, 1971; Johnson, 1970) and *Thlaspi* (Riley, 1956; Holmgren, 1971).

Isolating mechanisms. As a general rule, species of *Thelypodium* are either wholly or for the most part allopatric. Various types of isolation, such as seasonal, ecological, reproductive, and geographical operate to maintain well-defined species in the genus. Natural hybridization has not been detected. One of the most effective types of isolation is the geographical separation of species. As shown in Maps 1, 2, 4, and 5, the distributional ranges of the various taxa hardly overlap, and when this happens, other types of isolation seem to be effective. For example, *T. sagittatum* and *T. flexuosum* have different distributions (Map 4), but in northern Nevada, where they are both present, the latter species is found primarily in strongly alkaline desert flats and in association with shrubs, while the former species grows in meadows that are somewhat alkaline.

Seasonal isolation is generally considered to be "leaky," because it is not an absolute barrier and is likely to break down (Solbrig, 1970). The present writer has observed a few cases of contact between pairs of unrelated species of *Thelypodium* where seasonal isolation was evident and effective. In the examples mentioned below, plants of the first species of each pair were completely dry and some of them had shed most of their seeds, while those of the second species were at the beginning of their flowering season. These species pairs are as follows (including the collection numbers): *Thelypodium sagittatum* (6919) and *T. integrifolium* subsp. *integrifolium* (6920); *T. sagittatum* (6925) and *T. integrifolium* subsp. *complanatum* (6926); *T. flexuosum* (6936) and *T. integrifolium*

subsp. *complanatum* (6935); *T. howellii* subsp. *spectabilis* (6957) and *T. integrifolium* subsp. *complanatum* (6956); *T. laciniatum* (6968) and *T. integrifolium* subsp. *integrifolium* (6967).

Crossing experiments were done to a very limited extent, because it was not possible to bring plants of closely related species to flower at overlapping periods. The only results worth mentioning are those from the reciprocal crosses between *Thelypodium rollinsii* and two subspecies of *T. integrifolium* (subsp. *integrifolium* and *affine*). Nearly fifty flowers were crossed in each direction and no fruits were formed. This suggests that the two species are genetically isolated.

Seed dispersal. Seeds of *Thelypodium* are quite small and always very light in weight. The lightest seeds in the genus belong to *T. rollinsii* and *T. wrightii*, where the average weight of a single seed ranges between 0.15 and 0.18 mg. The heaviest seeds are found in *T. paniculatum* and *T. brachycarpum*, where the average weight ranges from 0.58 to 0.62 mg. Seed weight for the other species of the genus falls between the two sets of species given above but it is much closer to the former pair of species than to the latter.

Being very light in weight, the seeds of *Thelypodium* are probably very easily distributed. Wind may be an important factor in their dispersal in open habitats, such as deserts, flats, and open slopes, but the action of rain wash is perhaps equally, if not more, important in such open habitats. Flooding is likely to be significant in seed dispersal of species growing along streamsides, creek beds, and river banks and may also be important for those species found in meadows (Table 4).

Palynology

Based on light microscope studies alone, pollen grains were said to be similar throughout the Cruciferae. Erdtman (1952, 1969, 1971) suggested that the Cruciferae is ". . . a very stenopalynous family." The advantages of the scanning electron microscope (SEM) in palynological studies have been pointed out by Echlin (1968), who published one of the earliest known SEM photomicrographs of cruciferous pollen belonging to the genus *Cheiranthus*. Pollen SEM photomicrographs of other crucifers have been published by Martin and Drew (1969, 1970) and Stork (1972). These few reports suggest that some interesting differences in pollen grains of the genera studied do exist and the findings raised some questions on the validity of the conclusions reached by Erdtman from light microscopy alone. With this in mind, a comprehensive pollen survey of the Cruciferae, using the SEM is being conducted by R. C. Rollins, E. A. Shaw, J. E. Rodman and myself. The results will be published independently.

The pollen grains of the Cruciferae are said to be more or less similar to those of the Capparaceae and different from the Papaveraceae-Fumaroideae (Erdtman, 1951, 1971). It is generally agreed that the Papa-

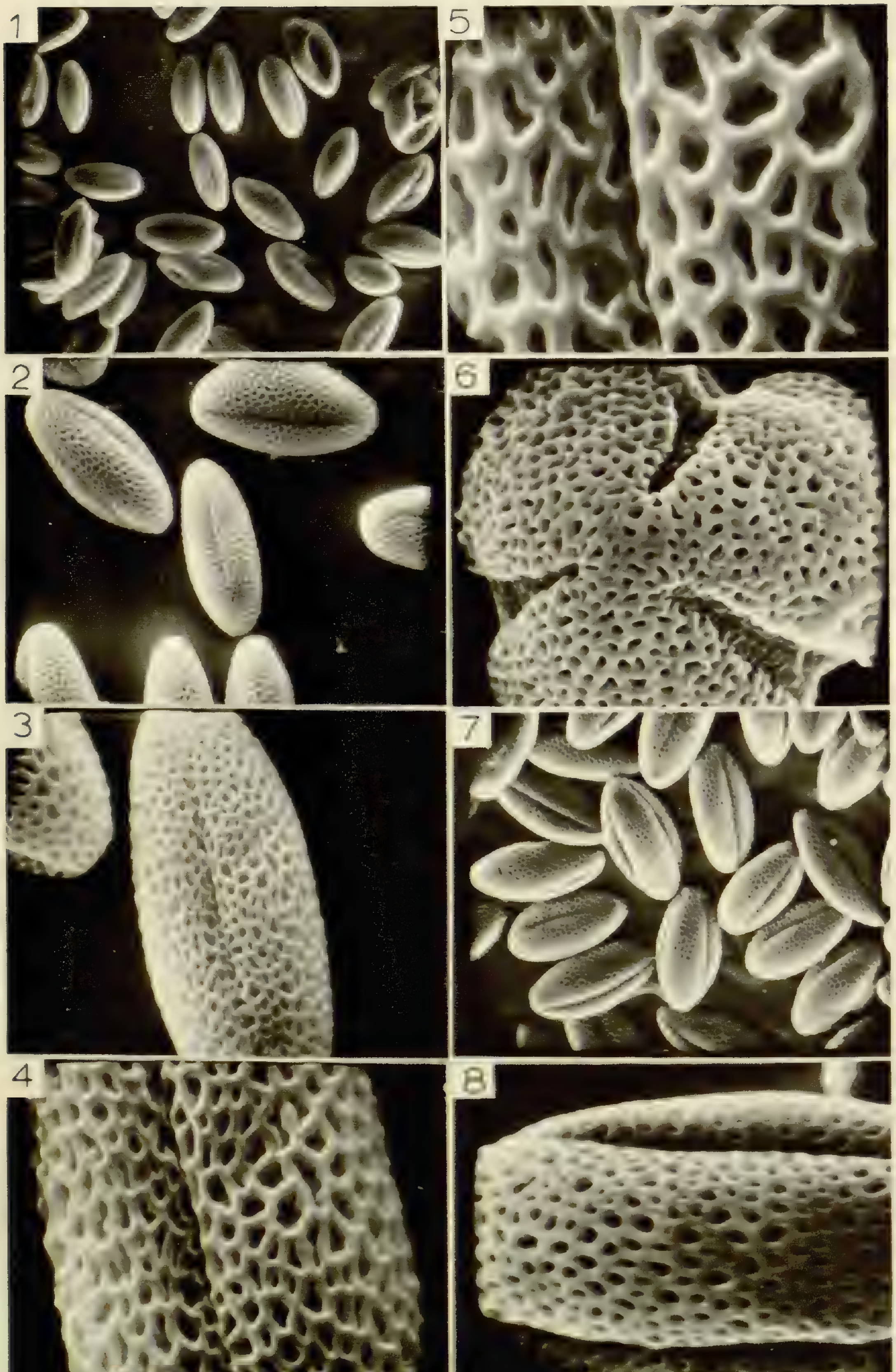


PLATE 10. SEM photomicrographs of pollen grains of *Thelypodium milleflorum*, Al-Shehbaz 6898 (FIGS. 1–6) and *T. stenopetalum*, Al-Shehbaz 6947 (FIGS. 7–8). Magnifications: 1. 490×; 2. 980×; 3. 2450×; 4. 4900×; 5. 9800×; 6. 5000× (acetolysed); 7. 700×; 8. 3500×.

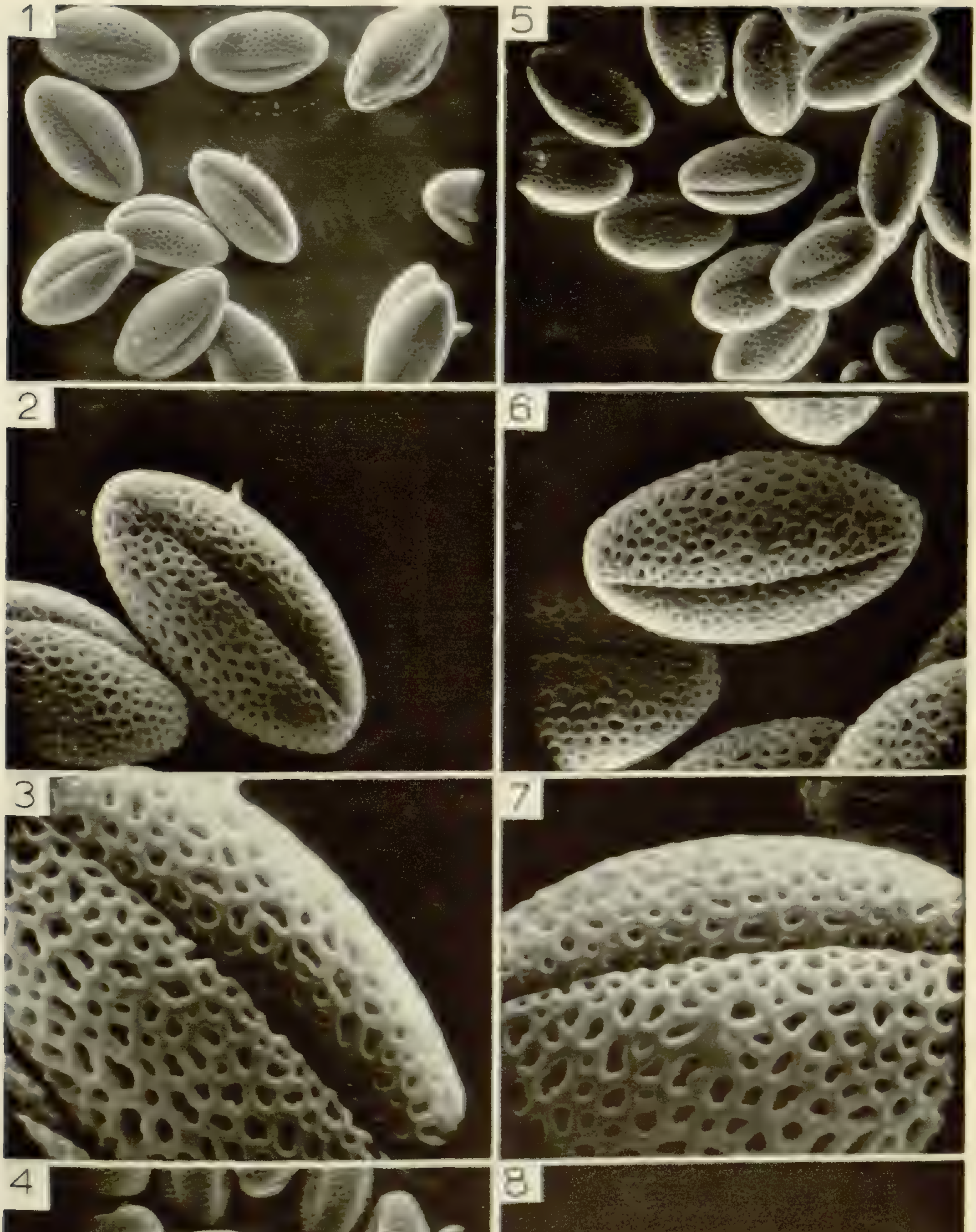


PLATE 11. SEM photomicrographs of pollen grains of *Thelypodium rollinsii*, Al-Shehbaz 6908 (FIGS. 1–3), *T. laxiflorum*, Al-Shehbaz 6912 (FIG. 4), *T. flexuosum*, Hitchcock & Muhlick 22292 (FIGS. 5–7), and *T. paysonii*, Rollins & Tryon 58296 (FIG. 8). Magnifications: 1. 760×; 2. 1900×; 3. 3800×; 4. 770×; 5. 750×; 6. 1875 ×; 7. 3750×; 8. 1700×.

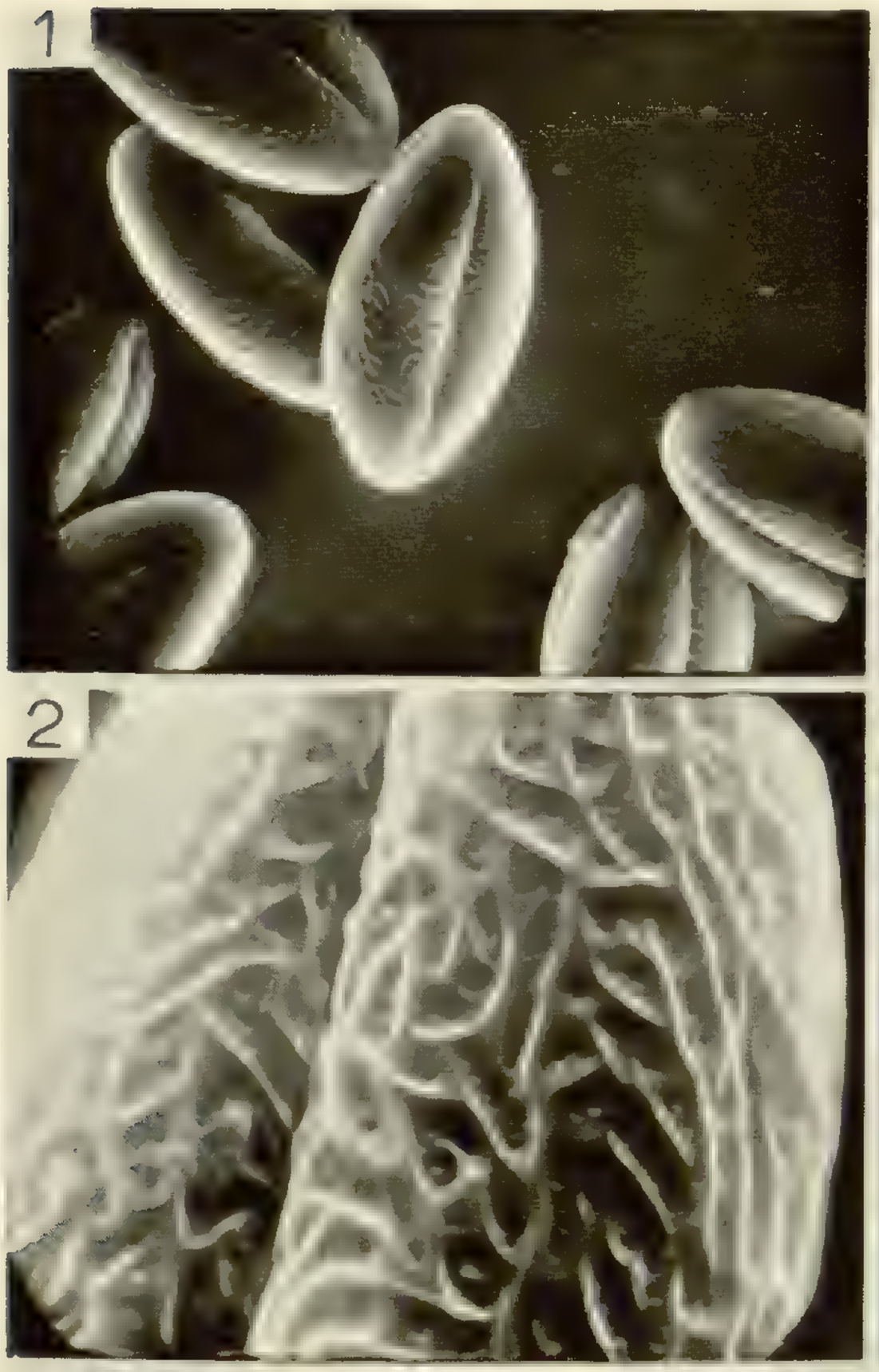
veraceae is not closely related to the other two families for morphological (Cronquist, 1968; Merxmüller & Leins, 1967) and chemical reasons (Hegnauer, 1964, 1969; Ettlinger and Kjaer, 1968). It has been suggested that the tribe Thelypodieae (Stanleyeae) is the link between the Cruciferae and the ancestral Cleomoideae-Capparaceae (Takhtajan, 1969). With the hope that pollen grains of the Thelypodieae and the Cleomoideae might give further insight into the relationship between the two families, a survey of all the genera of the Thelypodieae and selected genera of the Cleomoideae was conducted. Our findings on all the genera of the Thelypodieae will be presented in the comprehensive survey of the family mentioned above. *Thelypodium* is used as a representative of the tribe in the present discussion, since its pollen grains are fairly similar in many respects to most of the other members of the tribe. The terminology used follows that illustrated by Kremp (1965).

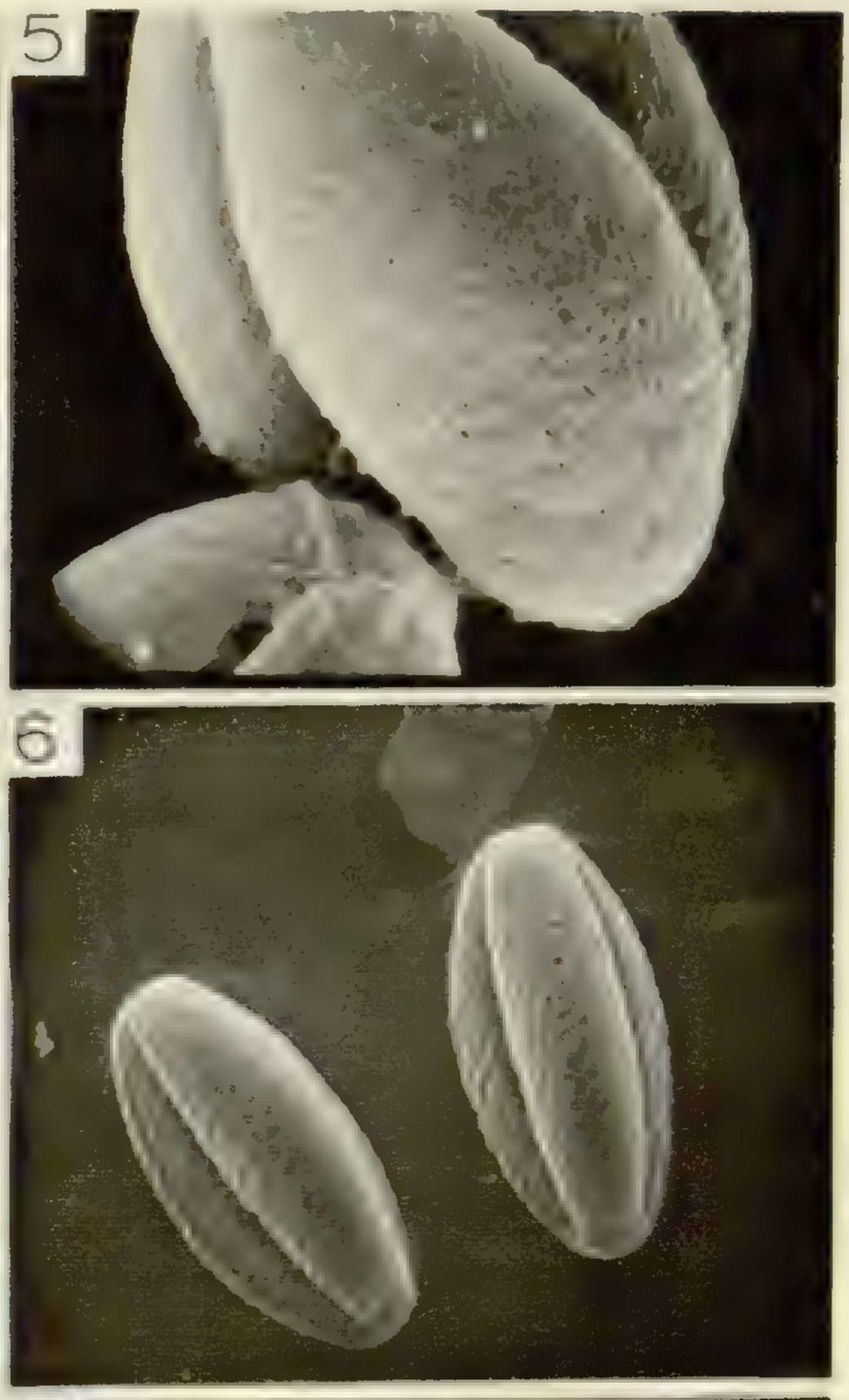
Pollen grains of all samples were taken from herbarium specimens and mounted, without treatment, on aluminum holders using double-stick tape. A very few samples of *Thelypodium* and *Cleome* were acetolized by Mr. Umesh Banerjee following the standardized method of Erdtman (1960). All samples were coated in a vacuum chamber with a thin film of carbon (50–100 Å thick) followed by a gold-palladium film (200–300 Å thick) for conductivity and to prevent charging. Polaroid photomicrographs were taken on an AMR Model 900 Scanning Electron Microscope.

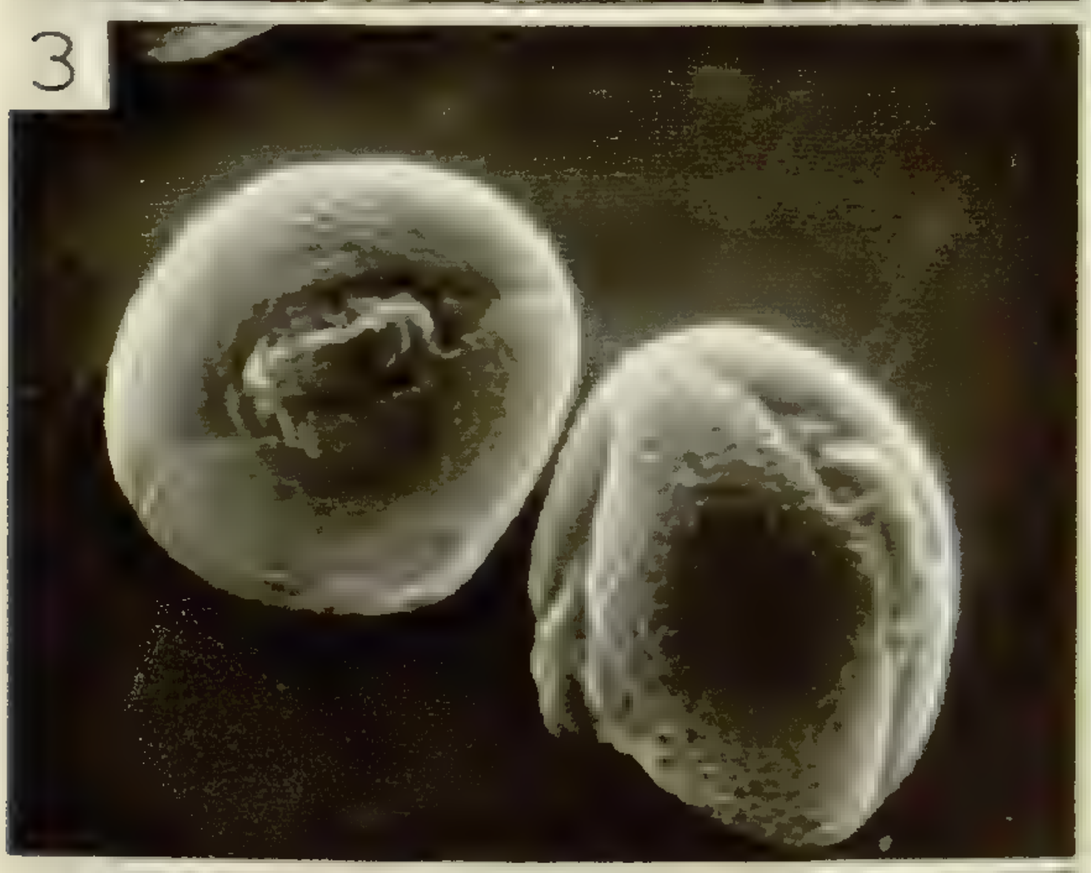
Pollen of Thelypodium. Like most genera of the Thelypodieae, *Thelypodium* species are fairly uniform in their pollen morphology (Plates 10 and 11). The following description is based on pollen of almost all species of the genus: pollen prolate, reticulate, tricolpate, 19–29 μ long, 9–15 μ wide, rounded at the poles; colpi rather long and nearly reaching the poles but remaining distinct (Plate 10, Fig. 6); reticulum smooth, fine in size; lumina rounded or seldom slightly angled, variable in size and shape, 0.1–1.5 (2.7) μ in diameter, smaller ones nearly isodiametric, larger irregular and sometimes elongated, the smaller lumina are nearer the polar region than the middle; reticulum distinctly elevated by supporting columellae that are sometimes visible, free columellae rare; muri 0.3–0.7 μ wide.

There is some degree of variability in the shape of the lumina. Those of *Thelypodium stenopetalum* are rounded, while those of *T. milleflorum* are slightly subangular (Plate 10, Figs. 4, 5, and 8). The description given, excluding measurements, presents a fairly good picture of the pollen in the Thelypodieae except the genera *Warea* and perhaps *Streptanthella* which have a decidedly coarser reticulum.

Pollen of certain Cleomoideae. Pollen of the family Capparaceae was said to show some variation in surface configurations by Erdtman (1952, 1971), but it was concluded by the same author (Erdtman, 1969) that the family is "markedly stenopalynous." Our preliminary studies of a few species of the family, most of which belong to the Cleomoideae, do not







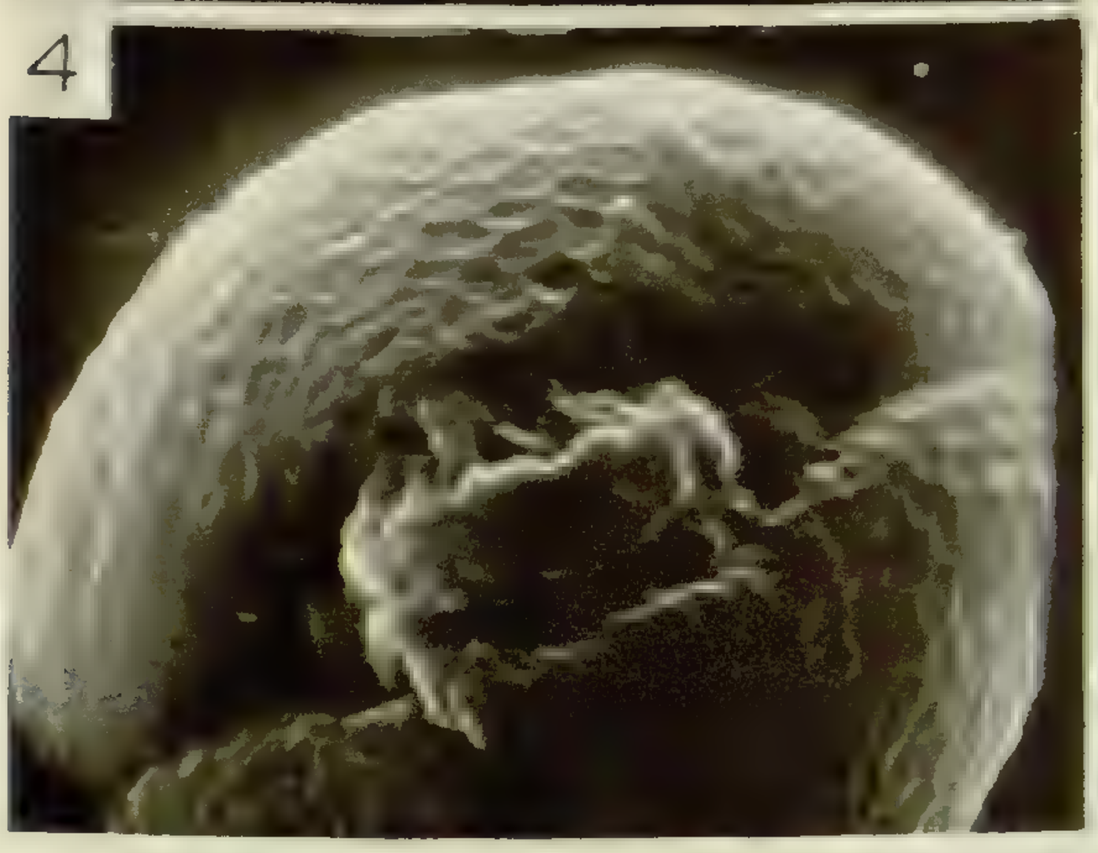
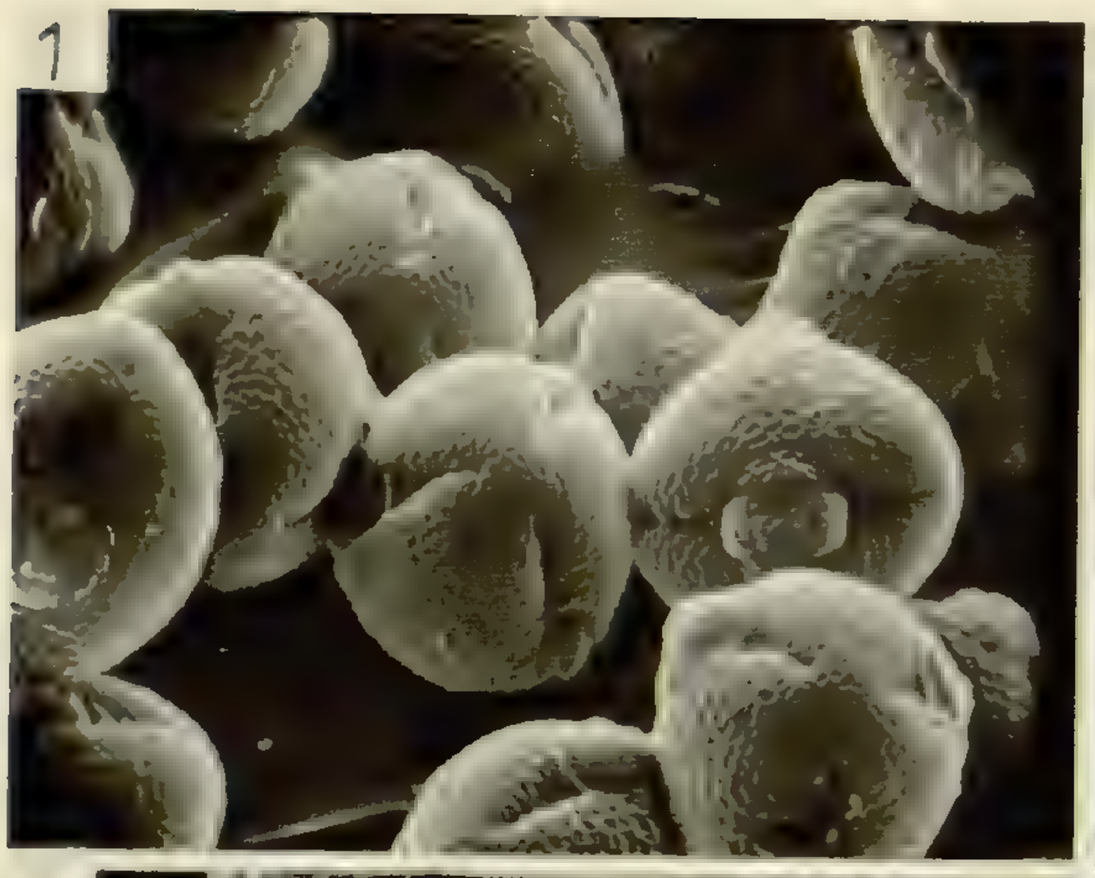
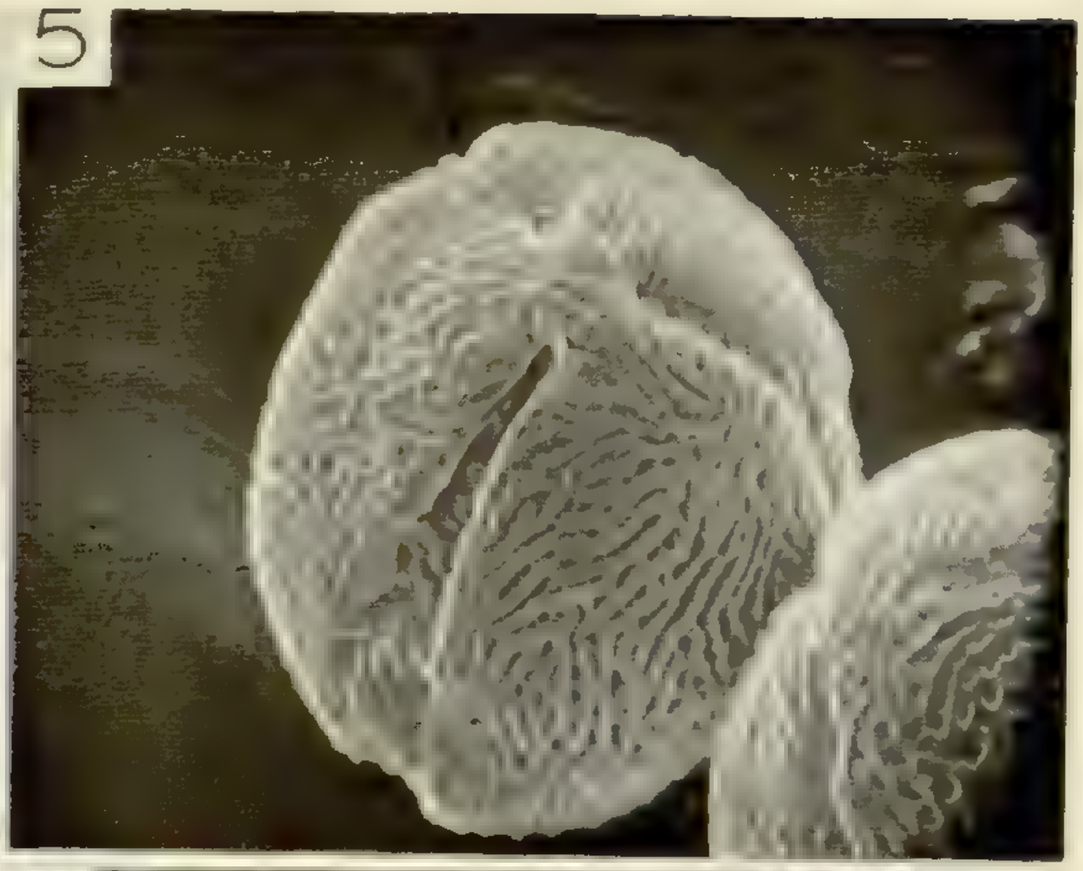
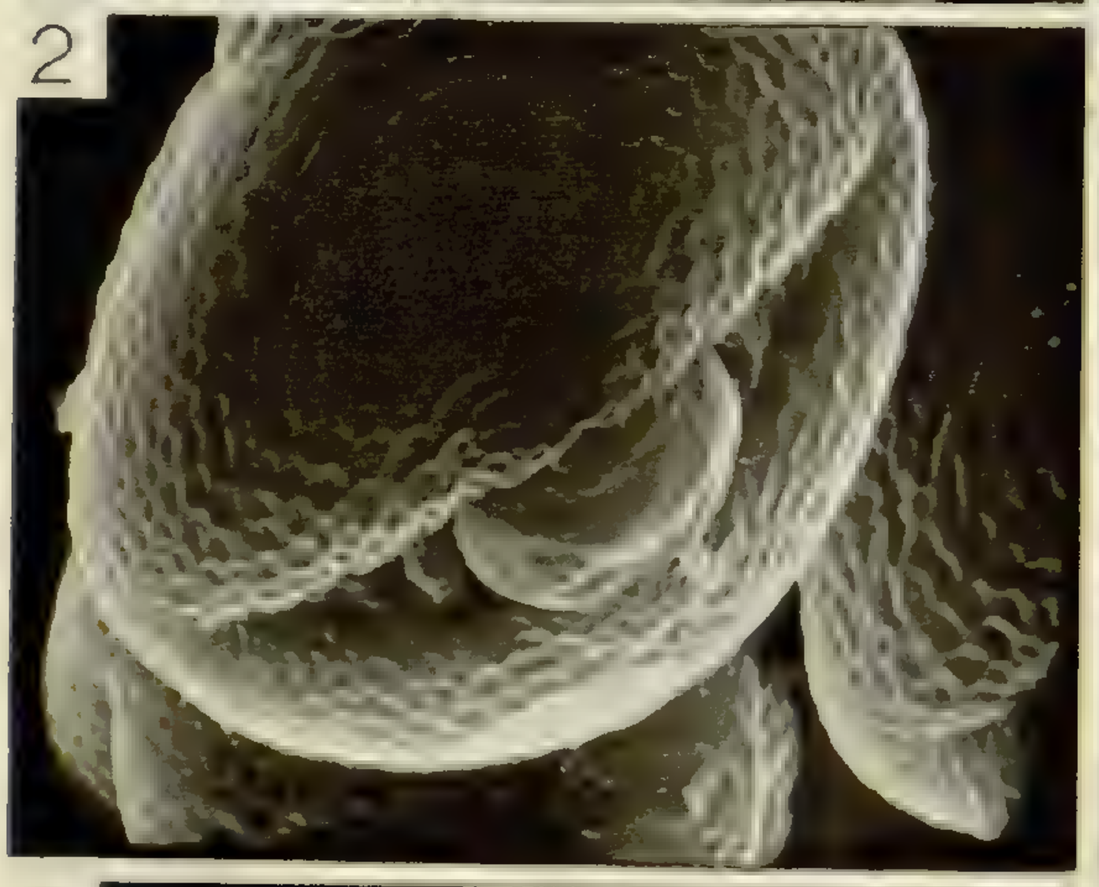
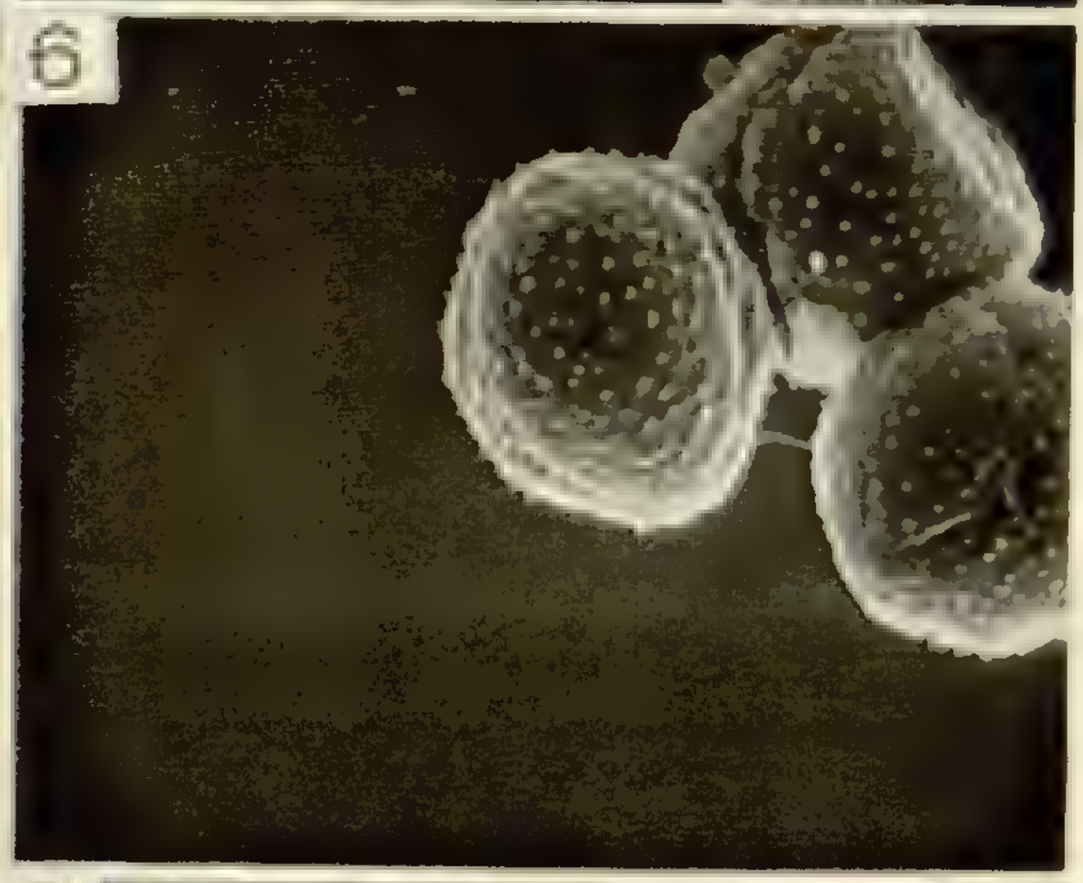


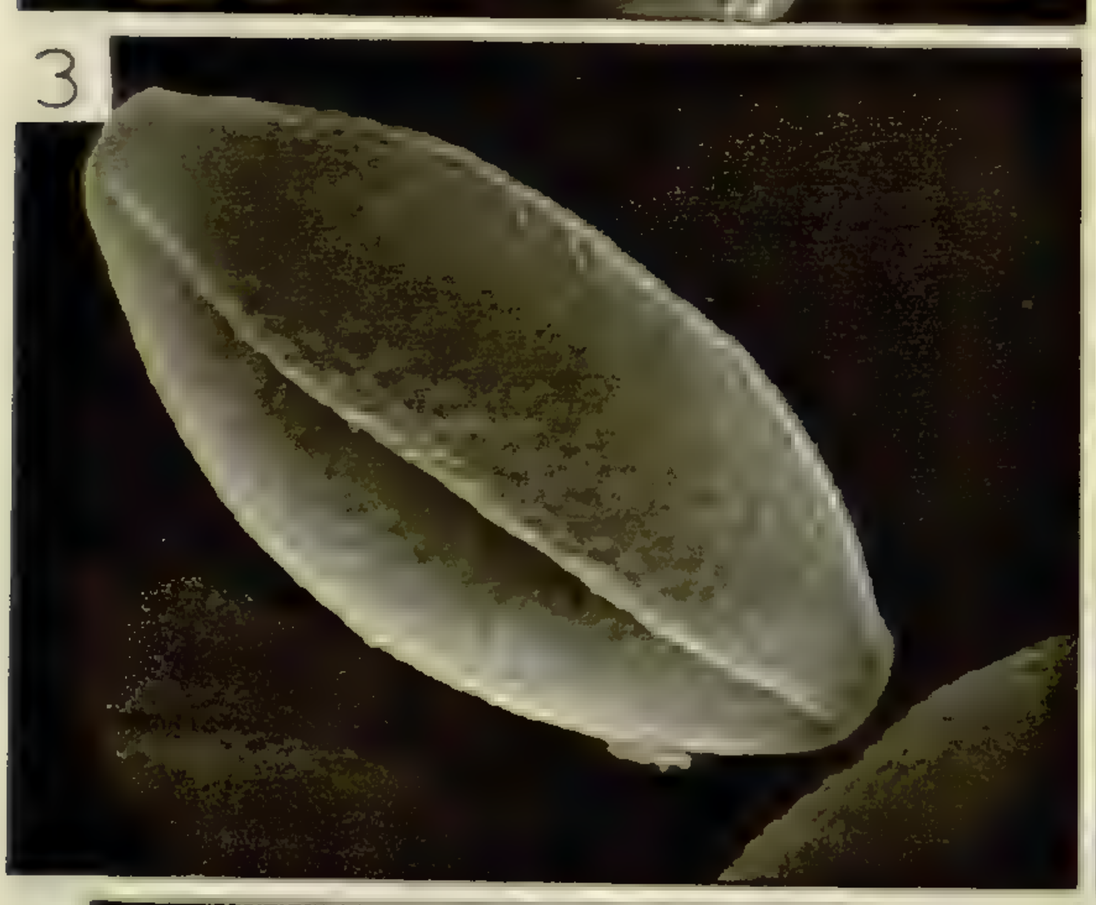
PLATE 12. SEM photomicrographs of pollen grains of selected genera of the Capparaceae. FIGS. 1–2. *Polanisia dodecandra*, Nelson s.n. 1931; FIGS. 3–4. *Oxystylis lutea*, Wiegand 803; FIG. 5. *Crataeva tapia*, Hutchison 2538 (acetolysed); FIG. 6. *Wislizenia retrofracta*, Peebles 14558; FIG. 7. *Isomeris arborea*, Munz 11941; FIG. 8. *Cleomella longipes*, Muller 1100. Magnifications: 1. 970×; 2. 4850×; 3. 1519×; 4. 3798×; 5. 2500×; 6. 990×; 7. 2083×; 8. 2450×.

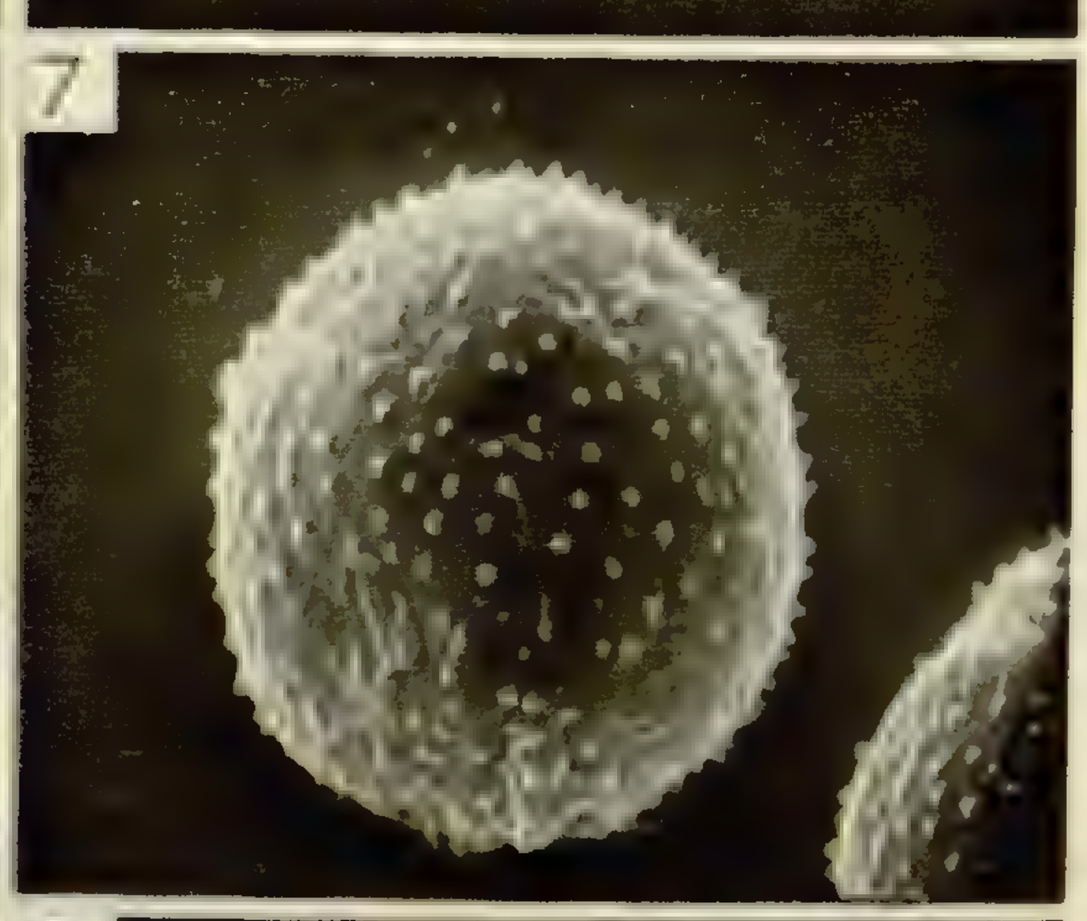


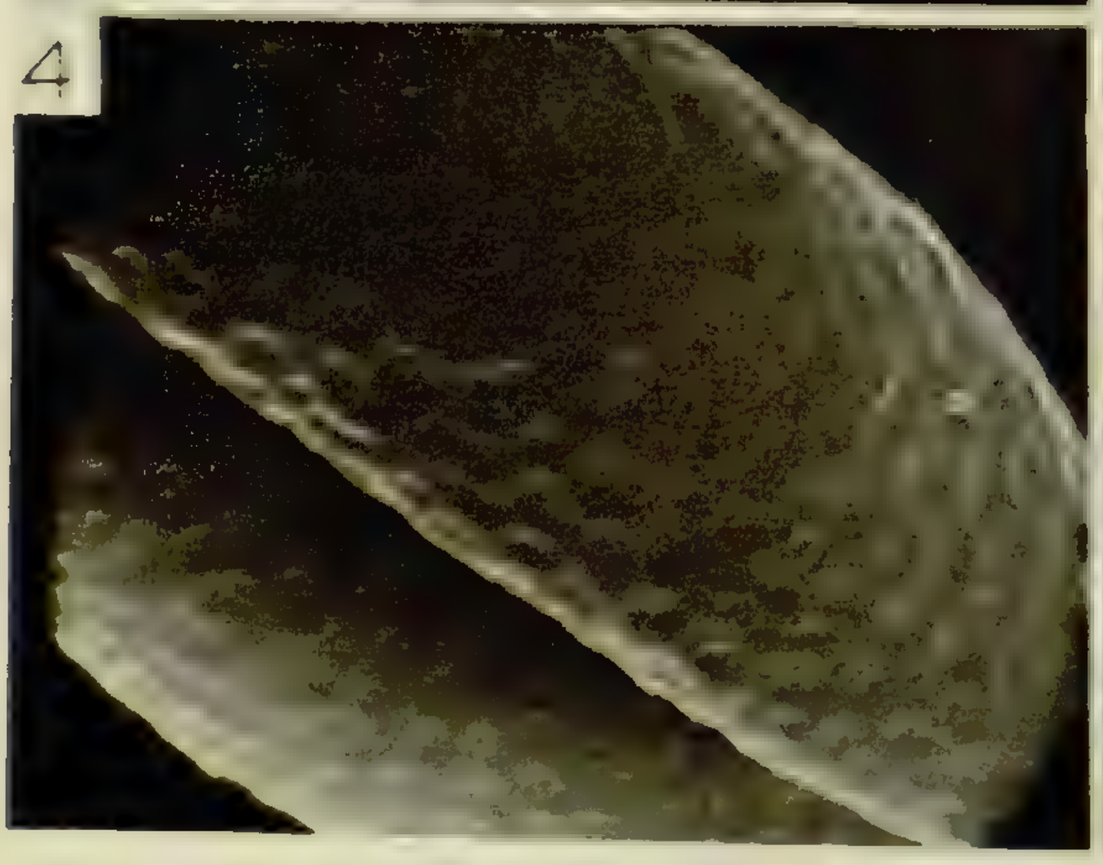












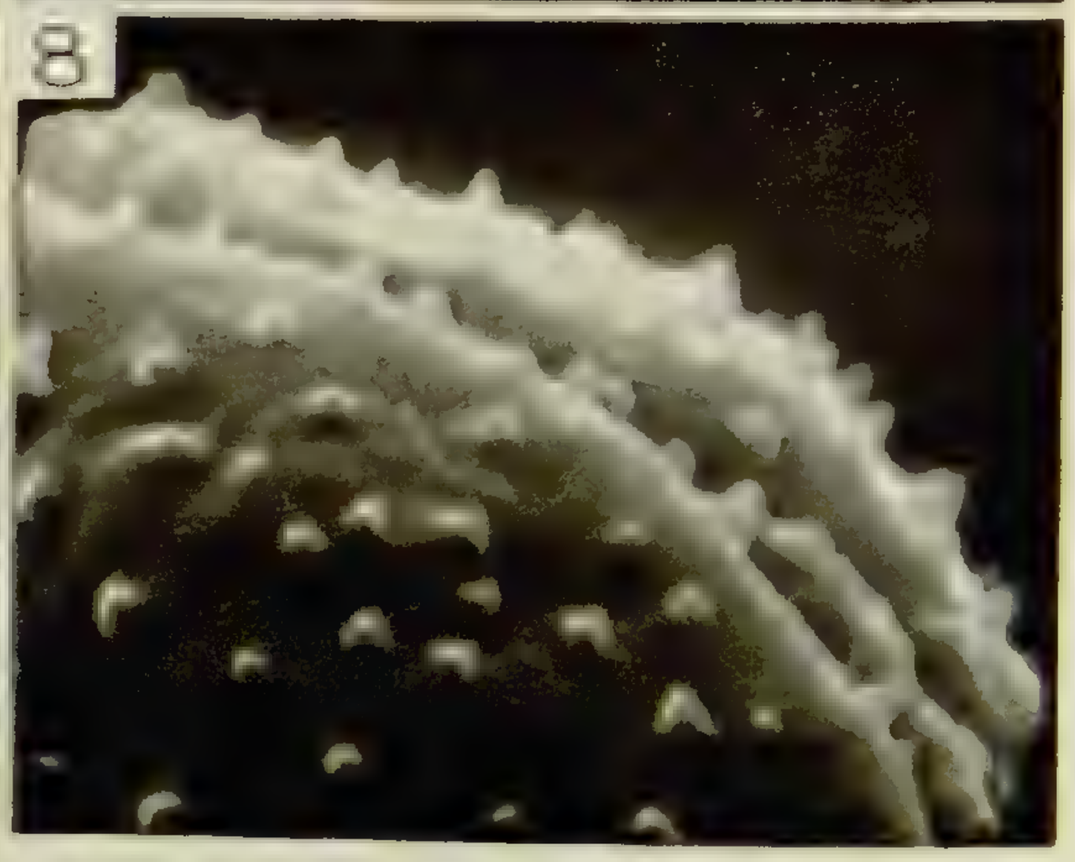
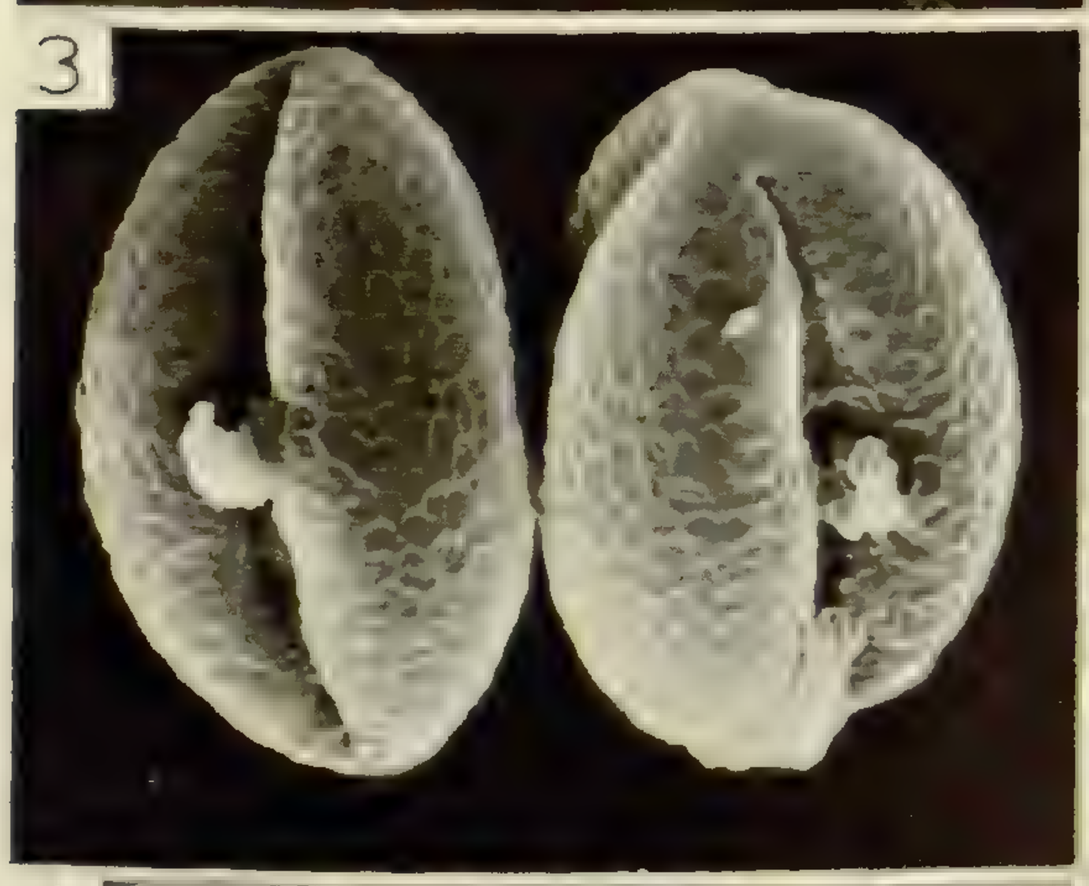
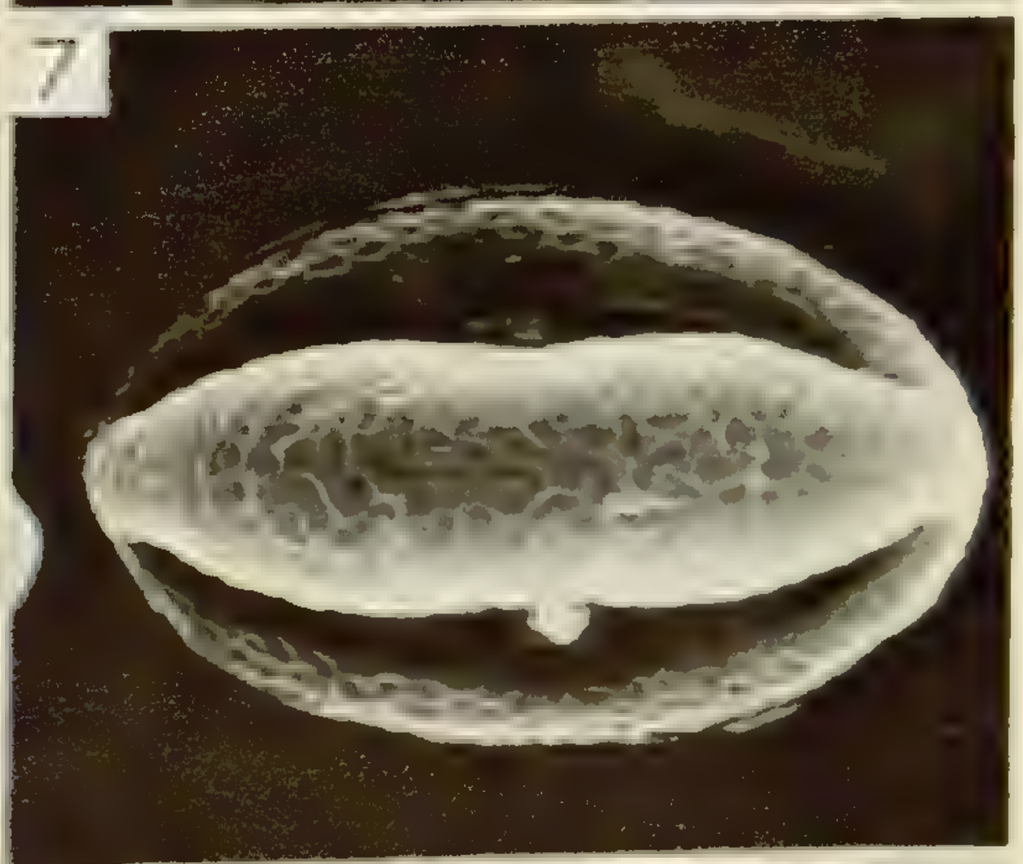


PLATE 13. SEM photomicrographs of pollen grains of certain species of *Cleome*. FIGS. 1–2. *C. muticaulis*, LeSueur 642; FIGS. 3–4. *C. serratula*, Smith 5660; FIG. 5. *C. gynandra*, Potter 5463; FIGS. 6–8. *C. hassleriana*, Tracy 8725. Magnifications: 1. 980×; 2. 2450×; 3. 2475×; 4. 4950×; 5. 2450×; 6. 970×; 7. 1698×; 8. 4850×.





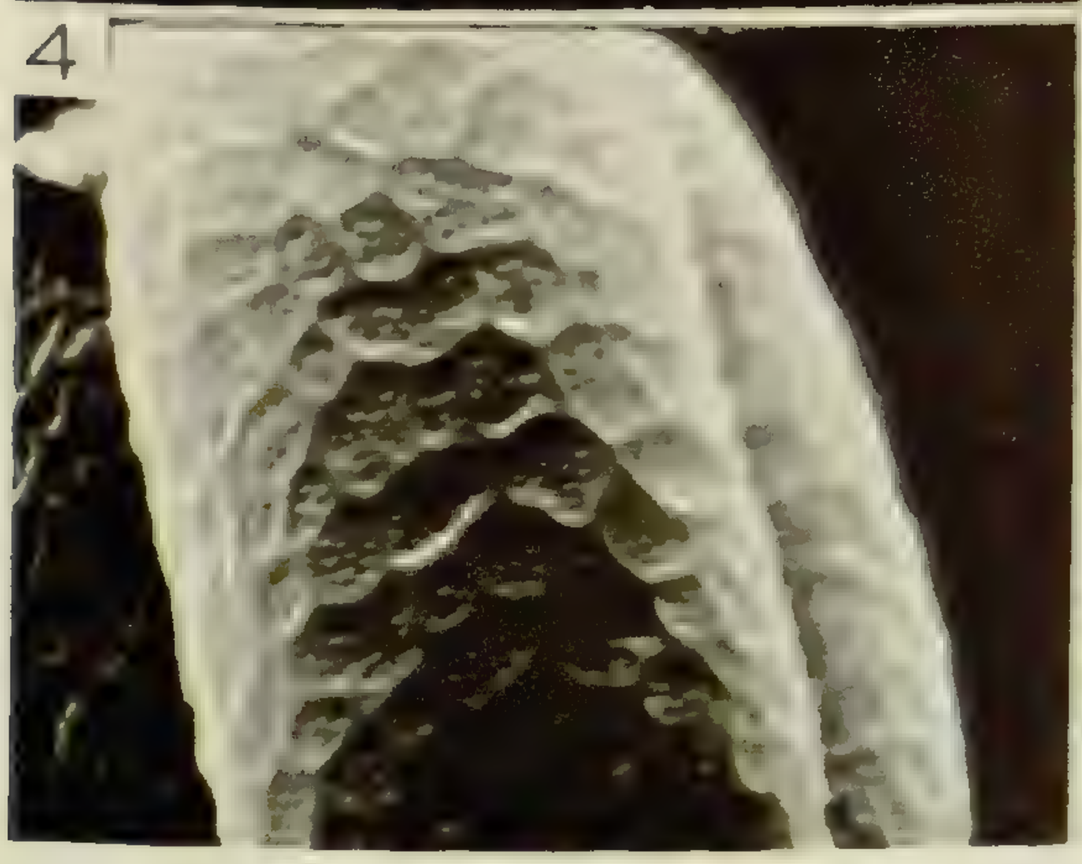


PLATE 14. SEM photomicrographs of pollen grains of certain species of *Cleome*. FIG. 1. *C. sparcifolia*, Kennedy 1991; FIGS. 2–4. *C. lutea*, Rollins 57261; FIGS. 5–8. *C. platycarpa*, Cronquist 7185. Magnifications: 1. 1800×; 2. 2450×; 3. 2500× (acetolysed); 4. 4900 ×; 5. 1000× (acetolysed); 6. 2500 ×; 7. 2500× (acetolysed); 8. 5000× (acetolysed).

support the last conclusion. All the genera discussed below except *Crataeva* belong to the subfamily Cleomoideae. The pollen of this genus is finely pitted (Plate 12, Fig. 5) and the unacetolized grains look nearly smooth.

Both *Polanisia dodecandra*, a native to the new world (Iltis, 1958), and *Cleome gynandra*, an introduced species from Africa (Iltis, 1960), have striate-reticulate pollen grains (Plates 12 and 13). The colpi in the two species extend nearly to the poles. The former species has prolate and the latter subspherical grains. In *C. hassleriana* the grains are distinctly echinate (Plate 13). Pollen grains of *C. platycarpa*, *C. serratula*, *C. sparsifolia*, *C. lutea*, *Isomeris arborea*, *Cleomella longipes*, and *Wislizenia refracta* are prolate, shallowly reticulate, and with shallow colpi extending nearly to the poles (Plates 12, 13, and 14). The muri, if the term is applicable here, are very low and the surface between them is distinctly pitted (Plate 14). The pollen is distinctly tricolporate in *C. platycarpa* and *C. lutea* (Plate 14), but *C. serratula* and *W. refracta* appear in Plates 12 and 13 as though they are tricolpate. However, the last two species are clearly tricolporate as judged from the study of their acetolysed pollen by light microscopy. The pollen grains of *C. muticaulis* and *Oxystylis lutea* resemble each other in being elliptical-subspherical, tricolporate, and faintly reticulate. The two species are not related. In fact, *O. lutea* is considered to be at the end of a reduction series in the order *Cleome*, *Cleomella*, *Wislizenia*, and *Oxystylis* (Iltis, 1957).

Although reticulate pollen grains are found in the Cleomoideae, they are very clearly different from those of the Cruciferae. The reticulum in the latter family is very sharply defined and clearly elevated by supporting columellae. The reticulum in the Cleomoideae, when present, is much shallower and neither the columellae nor the lumina are recognizable. Furthermore, the pitted surface between the "muri" in the Cleomoideae has not been detected in the Cruciferae. In addition to these significant differences, pollen of the Cruciferae are colpate, while the Cleomoideae appear to be exclusively colporate.

Two conclusions can be drawn from the comparison of pollen grains of the tribe Thelypodieae and the subfamily Cleomoideae and both are contrary to those reached by Erdtman (1969, 1971). First, the family Capparaceae is not a stenopalynous family. Second, pollen of the Capparaceae is very different from that of the Cruciferae. The similarities between them appear to be less significant than previously supposed. Pollen grains of the Thelypodieae are typically cruciferous and pollen data alone do not seem to support the suggestion that the tribe is intermediate between the rest of the Cruciferae and the Cleomoideae.

Cytology

Until recently, cytological information concerning the genus *Thelypodium* has been lacking. The only available report containing chromo-

some counts of species that are true members of the genus is that of Rollins (1966). An earlier report by Snow (1959) included a chromosome count of *T. lasiophyllum*, but the species is here excluded from *Thelypodium* and placed with its relatives in *Caulanthus*. Rollins presented for the first time counts on *T. flavescens* (*n*=14), *T. lemmonii* (*n*=14), *T. flexuosum* (*n*=13), *T. texanum* (*n*=13), and tentative counts on *T. laciniatum* (*n*=ca. 12) and *T. milleflorum* (*n*=ca. 14). Both *T. flavescens* and *T. lemmonii* are considered members of *Caulanthus* in the present treatment. We have been able to confirm the earlier chromosome count of *T. texanum* from greenhouse plants grown from seeds collected by A. S. Barclay (see below). The approximate numbers given by Rollins (1966) for *T. laciniatum* and *T. milleflorum* are very close to our finding of *n*=13 in both species.

All the chromosome counts presented here were made from bud materials fixed in three parts of 100% ethyl alcohol and one part glacial acetic acid. After one day of fixation, the buds were washed twice in 70% alcohol before they were stored or studied. The results are presented below.

Thelypodium crispum Greene ex Payson. *n*=13: Ormsby Co., Nevada. *I. & M. Al-Shehbaz 68110*, GH (Plate 15, Fig. 4).

Thelypodium howellii Watson subsp. *spectabilis* (Peck) Al-Shehbaz. *n*= 13: Union Co., Oregon. *I. & M. Al-Shehbaz 68151*, GH (Plate 15, Fig. 2).

Thelypodium integrifolium (Nutt.) Endl. subsp. *integrifolium*. *n*=13: Gunnison Co., Colorado. *I. & M. Al-Shehbaz 6903*, GH.

Thelypodium integrifolium (Nutt.) Endl. subsp. *affine* (Greene) Al-Shehbaz. *n*=13: Clark Co., Nevada. *I. & M. Al-Shehbaz 6988*, GH (Plate 15, Fig. 3).

Thelypodium laciniatum (Hook.) Endl. *n*=13: Mono Co., California. *I. & M. Al-Shehbaz 68112*, GH.

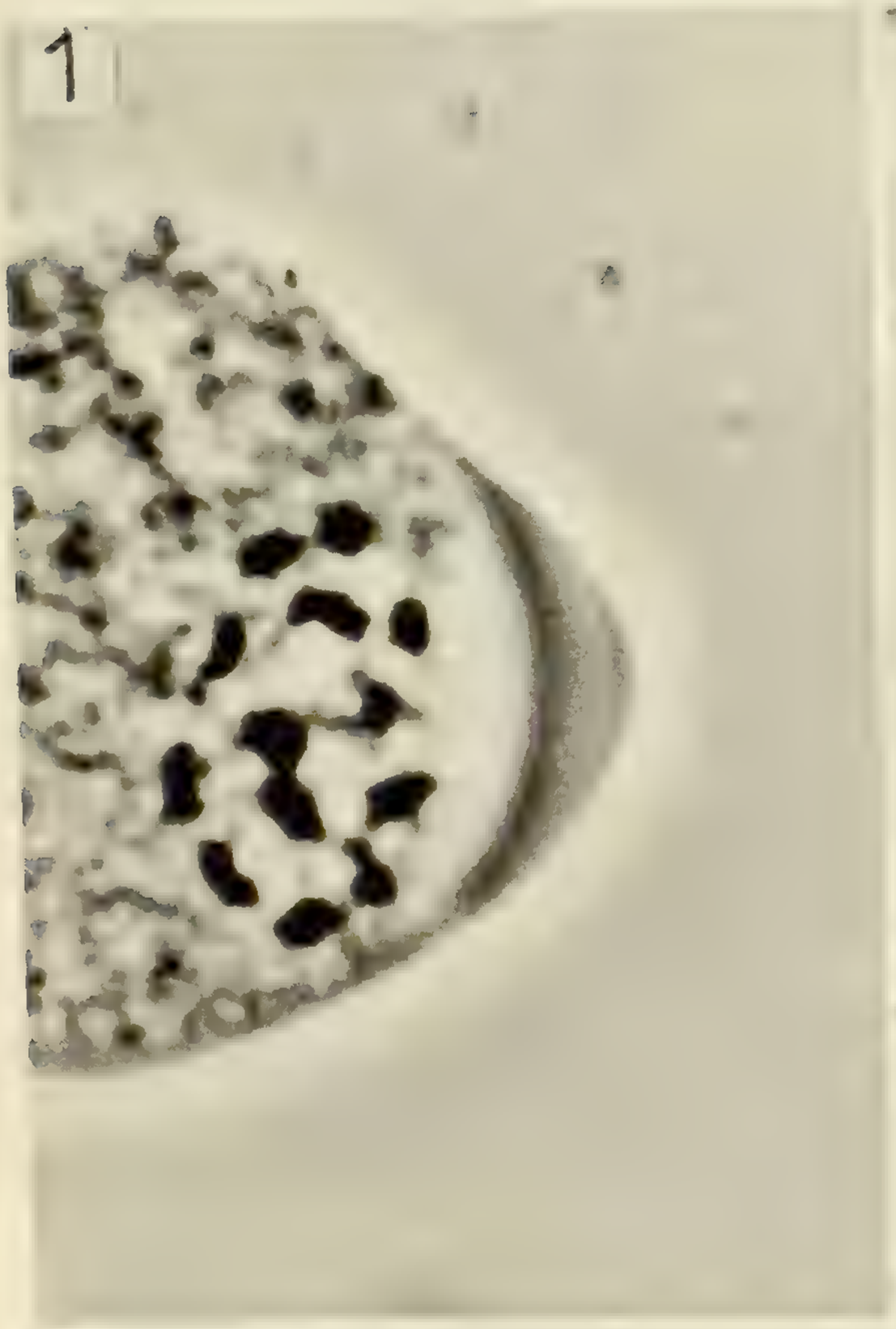
Thelypodium milleflorum Nelson. *n*=13: Elko Co., Nevada. *I. & M. Al-Shehbaz 6898*, GH.

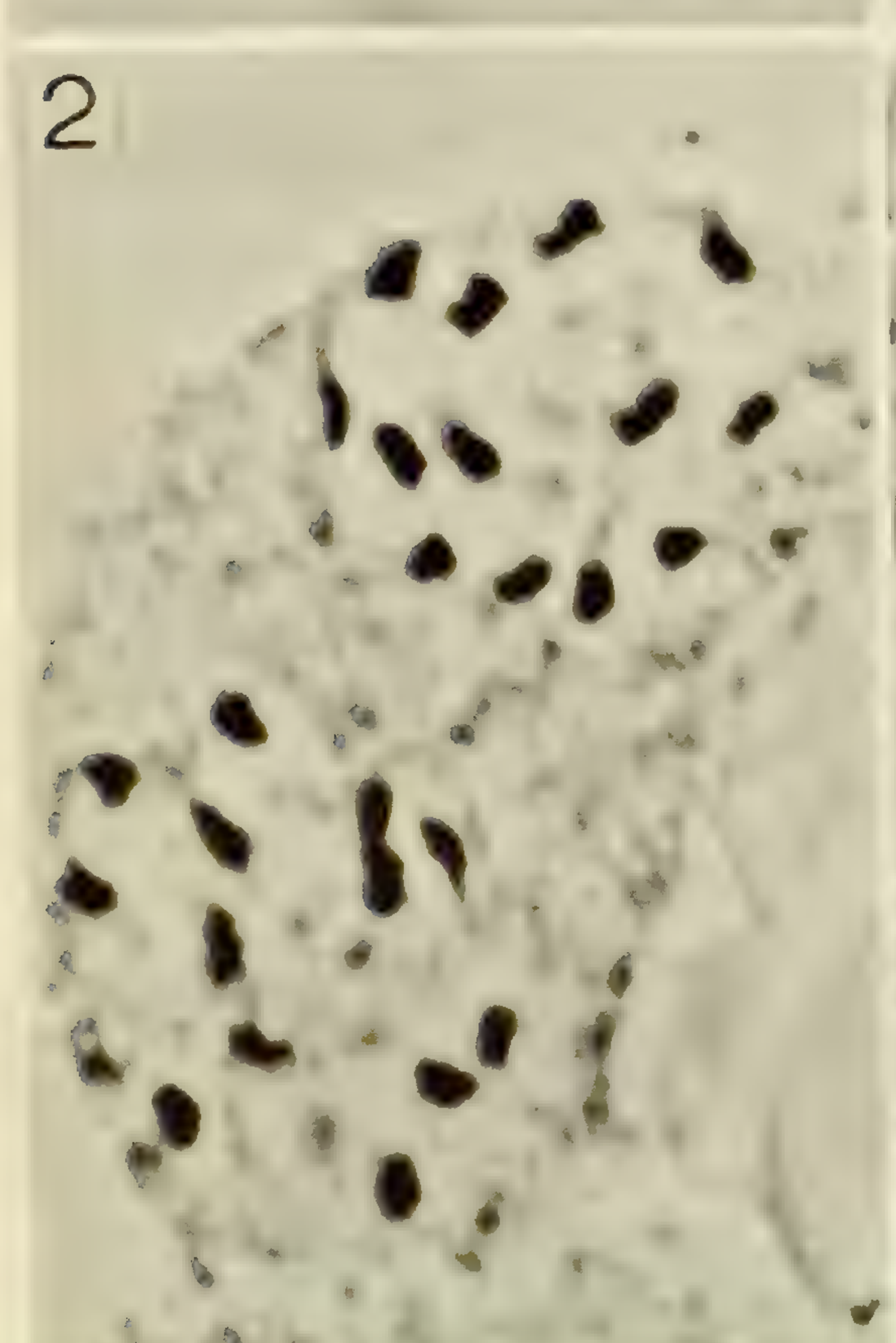
Thelypodium rollinsii Al-Shehbaz. *n*=13: Sevier Co., Utah. *I. & M. Al-Shehbaz 6913*, GH.

Thelypodium sagittatum (Nutt.) Endl. subsp. *ovalifolium* (Rydberg) Al-Shehbaz. *n*=13: Garfield Co., Utah. *I. & M. Al-Shehbaz 6911*, GH (Plate 15, Fig. 1).

Thelypodium texanum (Cory) Rollins. *n*=13: Brewster Co., Texas. From seeds collected by *A. S. Barclay 713*, GH.

It is very likely that the fundamental chromosome number for *Thelypodium* is *n*=13. More counts from the species listed above and the remaining members of the genus are needed before any rigid conclusions can be made. Although a haploid number of *n*=13 has not yet been counted from other genera of the tribe Thelypodieae, it is very close to *n*=14, which is the most common number in the tribe. The latter number is very common in *Streptanthus*, *Caulanthus*, *Stanleya*, and the monotypic





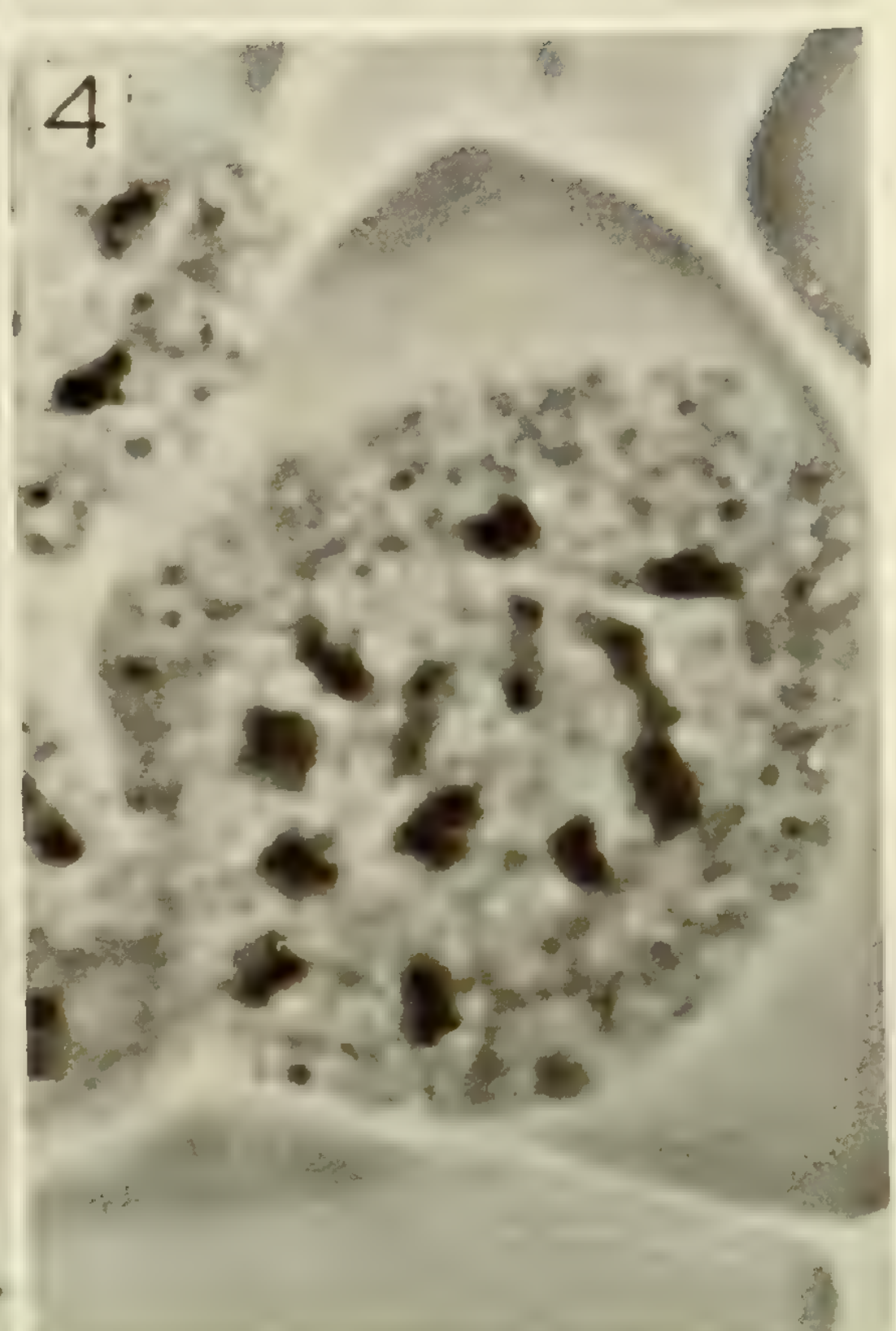


PLATE 15. Chromosomes of selected species of *Thelypodium*. FIG. 1. PMC, half of anaphase I, *T. sagittatum* subsp. *ovalifolium*, Al-Shehbaz 6911; FIG. 2. PMC, late anaphase I, *T. howellii* subsp. *spectabilis*, Al-Shehbaz 68151; FIG. 3. PMC, half of anaphase I, *T. integrifolium* subsp. *affine*, Al-Shehbaz 6988; FIG. 4. PMC, diakinesis, *T. crispum*, Al-Shehbaz 68110. All figures × ca. 2800.

Streptanthella. The least common numbers in the tribe appear to be n=10, present in two species of *Caulanthus*, and n=11 which is found in two species of *Thelypodiopsis* (Rollins, 1966; Rollins and Rüdenberg, 1971). Both *Thelypodiopsis linearifolia* and *T. ambigua* are listed as species of *Sisymbrium* in the two treatments, but, as suggested by these authors, the two species are out of place in *Sisymbrium*. Twenty-nine of the 50 species known cytologically (including the counts of *Thelypodium* presented here) that belong to the tribe *Thelypodieae* have chromosome numbers based on n=14 (Rollins, 1966; Rollins and Rüdenberg, 1971; Bolkhovskikh *et al.*, 1969). The presence of such a number in the three species of *Stanleya*, which is probably one of the most primitive genera of the tribe, and the occurrence of n=13 in nine species of *Thelypodium* is of interest. It is probable that a number of x=7 is basic for the tribe Thelypodieae. Furthermore, chromosome counts from other genera, such as *Romanschulzia*, *Warea*, and *Chlorocrambe*, as well as additional species of *Stanleya*, *Thelypodium*, *Streptanthus*, *Caulanthus*, and *Thelypodiopsis* are very necessary before one can present a clear picture of the cytology of the tribe.

Biochemical Systematics

Thelypodium, like many other primitive genera of the family Cruciferae, has received only minimal attention in general surveys of natural products. As far as the literature shows, only one species of *Thelypodium* (*T. texanum*) has been investigated for mustard oil glucosides (Daxenbichler *et al.* 1964) and seed proteins and fatty acids (Mikolajczak *et al.* 1961; Jones and Earle, 1966). Using paper chromatography, Dr. Martin G. Ettlinger and Charlyne P. Thompson (personal communication) analyzed seed samples of two species of *Thelypodium* (*T. texanum* and *T. milleflorum*) for their glucosinolate contents. Their results agree completely with those I have obtained by paper chromatography on these two species.

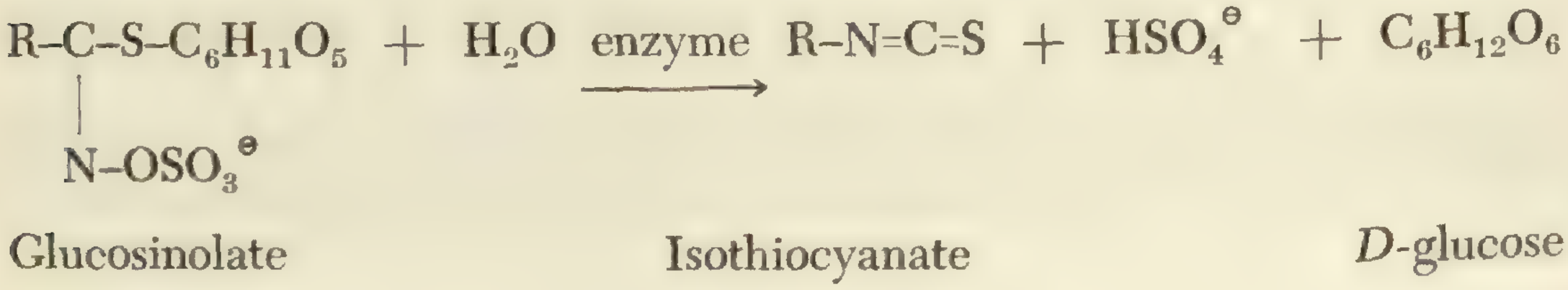
The mustard oil glucosides (glucosinolates) represent a unique class of natural products, restricted in their distribution to a limited number of families of the dicotyledons. The distinctive pungent flavor or odor present in some of the common mustards (species of *Brassica*, *Sinapis*, and other related genera) has been recognized for several centuries, and a few species have been utilized in the preparation of condiments (Vaughan and Hemingway, 1959). The flavoring principles (mustard oils or isothiocyanates) are only found in minute quantities, if at all, in the intact plant tissues, but are readily recognized when the tissues are crushed or injured (Ettlinger and Kjaer, 1968; Tang, 1971).

The glucosinolates are present in practically all the species of the family Cruciferae (Kjaer, 1960). Other families known to contain them are the Capparaceae, Tovariaceae, Resedaceae, Moringaceae (these five fam-

ilies constitute the well-defined order Capparales *sensu* Cronquist (1968), Limnanthaceae, Caricaceae, Tropaeolaceae, Gyrostemonaceae, Salvadoraceae, and the genus *Drypetes* (including *Putranjiva*) of the family Euphorbiaceae (Ettlinger and Kjaer, 1968).

Fifty glucosinolates were structurally known in 1968 (Ettlinger and Kjaer, 1968). Since then an additional 19 have been discovered from natural sources (cf. Elliott and Stowe, 1970; Gmelin *et al.* 1970; Kjaer and Schuster, 1970, 1971, 1972a, 1972b, 1973; Kjaer and Wagnières, 1971; Underhill and Kirkland, 1972).

The general formula of the glucosinolates was established by Ettlinger and Lundeen in 1956. The side chain (R) can be any organic group from methyl up (Ettlinger and Kjaer, 1968). As shown below, the glucosinolates are hydrolysed by myrosinase to isothiocyanates (mustard oils), sulfate, and *D*-glucose.



Many of the isothiocyanates volatilize readily. However, those containing sulfoxide (SO) or sulfone (SO_2) groups volatilize only with difficulty. Moreover, isothiocyanates that have a hydroxyl group on a carbon atom next to the one bearing the isothiocyanate group are neither volatile nor stable, and spontaneously cyclize giving rise to oxazolidine-2-thiones. The oxazolidine-2-thiones, among other glucosinolate derivatives, are known to have antithyroid or goitrogenic effects in man and a few other animals (Astwood *et al.* 1949; Langer, 1966; Van Etten *et al.* 1969; Gillie, 1971).

Nothing is known about the exact functions of the glucosinolates in the plants that contain them. Whittaker (1970) and Wareing (1965) suggested that they are probably seed germination inhibitors, while Kutáček (1964) and Elliott and Stowe (1971) proposed a function in the nature of allelopathy. Finally, the glucosinolates are said to have a defensive function against certain animal species (Fraenkel, 1959; Whittaker, 1970). The idea may have merit, but we know of certain species of insects that seem to have evolved to withstand any toxic effects exerted by the glucosinolates or their derivatives (Whittaker and Feeny, 1971; Ehrlich and Raven, 1964). In fact, it has been shown that these compounds stimulate feeding and oviposition in certain species of the insect genera *Pieris* and *Plutella* (Thorsteinson, 1953; Gupta and Thorsteinson, 1960; Nayar and Thorsteinson, 1963; Dethier, 1970; Schoonhoven, 1968, 1969).

The skeletal similarities between the glucosinolates and some of the

protein amino acids were clarified by Ettlinger and Lundeen (1956). We now know that these amino acids are direct precursors of the glucosinolates, and that glucosinolates may also be derived from higher homologues of protein amino acids, produced by a chain-lengthening mechanism utilizing acetate (Underhill *et al.*, 1962; Underhill and Wetter, 1966; Ettlinger and Kjaer, 1968; Josefsson, 1971).

Very little is known about the chemosystematic value of the glucosinolates. The first attempt to determine this value was made by Kjaer and Hansen (1958) with four species of the cruciferous genus *Arabis*. Using paper chromatography, Ettlinger and Thompson (1962) investigated a large number of cultivars belonging to a relatively few species of the genus *Brassica* and related genera. Their results showed certain distributional patterns of the glucosinolates in these taxa, but the most significant differences were between *Brassica* and *Sinapis*. The present investigation was conducted with the hope that the distribution of the glucosinolates within *Thelypodium* might provide some information of chemotaxonomic value, particularly in connection with certain species complexes.

Experimental. The paper-chromatographic analysis involves the enzymatic hydrolysis of the glucosinolates by myrosinase (in the presence of sodium ascorbate as a co-factor, 5 ml. of distilled water, and 100 ml. of diethyl ether) to isothiocyanates. Small portions of the ether extract of the isothiocyanates are checked for the presence of *p*-hydroxybenzyl isothiocyanate and oxazolidine-2-thiones. The remainder is converted into thioureas by the addition of ⅓ of its value of ethanolic ammonium hydroxide. The thioureas and oxazolidine-2-thiones are then chromatographed with the reference standard phenylthiourea in a few solvent systems (one to six), depending on the nature of these compounds. The extraction of the glucosinolate derivatives from the seeds, the paper chromatography techniques, and the solvent systems are essentially the same as those used by Ettlinger and Thomson (1962) and Ettlinger *et al.* (1966) and therefore will not be described again. The thioureas and oxazolidine-2-thiones were identified by comparing their R_{Ph} values (the ratios between the distances travelled by the thioureas and oxazolidine-2-thiones and by the phenylthiourea standard (Kjaer and Rubinstein, 1953)) with those of known compounds from tables kindly provided by Dr. Martin G. Ettlinger (Ettlinger and Thompson, unpublished results). Several standards of the thioureas, oxazoeidine-2-thiones, and isothiocyanates were generously given by Dr. Ettlinger.

The extraction of the glucosinolates from the leaves was as follows. Fresh rosette leaves (20–30 grams) were put into 500 ml. of boiling 70% methanol for 15–20 minutes. The leaves were blended for one to two minutes in a high-speed blender. They were then filtered through a few layers of cheesecloth, and the filtrate was boiled on a hot plate until all

of the methanol and most of the water had evaporated. After cooling, 10 ml. of distilled water was added. The diluted extract was then washed four to six times with generous portions of petroleum ether until most of the chlorophyll and other pigments were removed. The nearly colorless water extract of the glucosinolates was hydrolized and converted to the thiourea derivatives as outlined by Ettlinger and Thompson (1962) and Ettlinger *et al.* (1966). The thioureas and oxazolidine-2-thiones were then identified by paper chromatography as mentioned earlier.

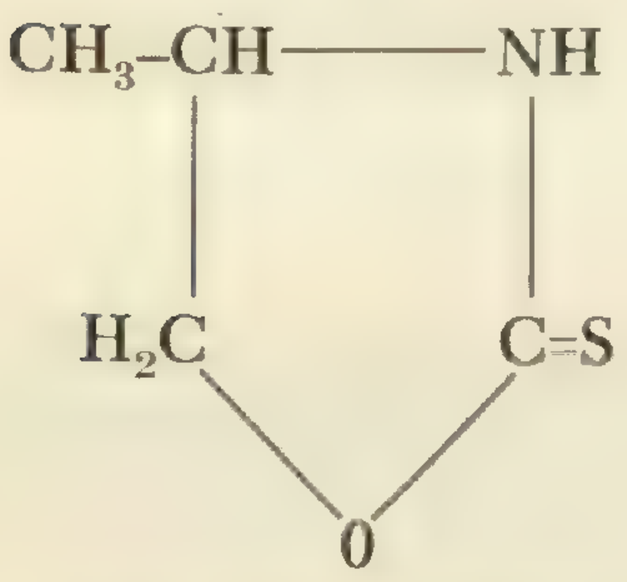
The extraction of the isothiocyanates for GLC analysis was as follows. Seeds (0.5 gm.) were finely ground and defatted with 75 ml. of diethyl ether for two to three hours. The ether was decanted carefully, and the ground seed was washed with 20–25 ml. of ether, filtered off, and washed three or four more times with ether on the filter. The defatted seed powder was air-dried and put in a 50 ml. Erlenmeyer flask, and 30 ml. of boiling 70% methanol was added. The flask was placed on a hot plate for approximately 15 minutes until the seed extract was freed of the methanol and some of the water. The concentrated extract was cooled and subjected to enzymatic hydrolysis by the addition of three drops of myrosinase preparation, 0.1 ml. of sodium ascorbate solution, 5 ml. of distilled water, and 10 ml. of diethyl ether (free of alcohol and peroxide). The mixture was let stand 10–12 hours at room temperature, in the dark, with occasional shaking. The ether extract, containing the isothiocyanates (and oxazolidine-2-thiones), was carefully removed from the aqueous mixture by pipette and used in the GLC analyses.

Boiling the samples in methanol was necessary to denature the various enzymes present in the seeds that might convert the glucosinolates or other substrates to volatile products other than isothiocyanates. Such products, which appeared as peaks of various sizes in a number of samples, were completely eliminated when the samples were boiled.

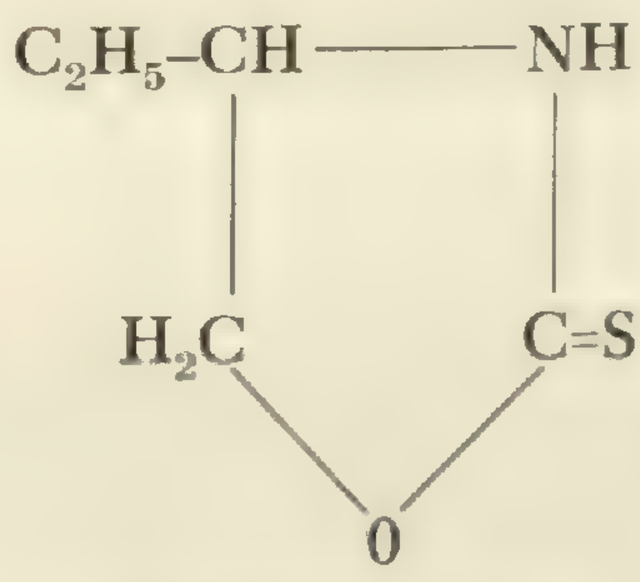
An F. & M. high efficiency gas chromatograph Model 402 linked with a Hewlett-Packard recorder Model 7127A was used in all analyses. The chromatograph was operated isothermally at a column temperature of 80° C. for the characterization of the highly volatile isothiocyanates (flame detector temperature was 145° C. and flash heater 130° C.), and at 160° C. for the characterization of those less volatile (temperatures of the flame detector and flash heater were 170° C. and 200° C. respectively). These isothiocyanates are shown in Table 8. The gas chromatograph was equipped with a hydrogen flame ionization detector. A U-shaped glass column (6 feet × ¼ inch) packed with 6% DC-560 and 2% EGSP-Z on 100/200 Gas-Chrom Q (Applied Science Laboratories) was used. The helium (carrier gas) flow rate was approximately 60 ml. per minute. A range of 10^2, an attenuation of 1, and a recorder speed of ¼ inch/minute were used. The sample size was 2μl. for the most part. The quantitative determination of the volatile isothiocyanates was accomplished by calculat-

ing their peak areas (done by the multiplication of their peak heights by the peak widths at half the height) as a measure of their amounts, which are expressed as percentages of the total volatile contents area. No attempts were made to quantify the oxazolidine-2-thiones, although it is possible to do so by UV absorption as described by Youngs and Wetter (1967).

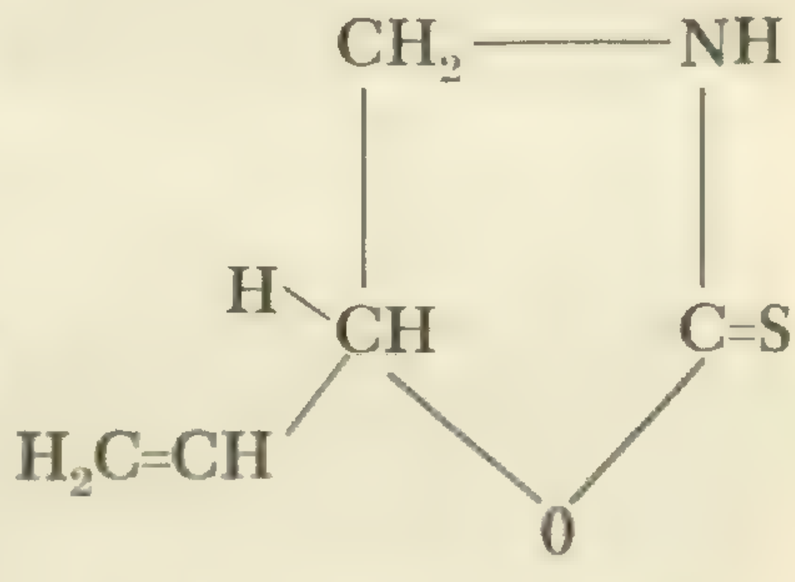
Results and discussion. A relatively large number of glucosinolates have been identified from the various species of *Thelypodium* (Table 5). None of the *p*-hydroxybenzyl glucosinolate has been detected in any of the samples prepared for paper-chromatographic analysis. Three oxazolidine-2-thiones encountered in *Thelypodium* are 4-methyloxazolidine-2-thione, 4-ethyloxazolidine-2-thione, and 5-vinyloxazolidine-2-thione, as shown below. These are derived from spontaneous cyclization of the isothiocyanates resulting from hydrolysis of the glucosinolates 2, 5, and 12 respectively. Each of these three glucosinolates is a very close relative of the one preceding it in Table 5.



4-Methyloxazolidine-2-thione



4-Ethyloxazolidine-2-thione



5-Vinyloxazolidine-2-thione

Two stereochemical configurations are known for the 2-hydroxy-3-butenyl glucosinolate and the derived 5-vinyloxazolidine-2-thiones. Astwood *et al.* (1949) discovered the first 5-vinyloxazolidine-2-thione in the genus *Brassica*. It was shown later to be the (S) compound by Kjaer *et al.* (1959). The (R) isomer was obtained from the seeds of *Crambe abyssinica* by Daxenbichler *et al.* (1965). No attempts have been made in the present treatment to determine which isomer is produced in *Thelypodium*.

The results of the paper-chromatographic analyses are shown in Table 6. The comparison between these and the GLC results in Tables 9, 10, 11, and 12 shows that some of the minor constituents found in a number of species were not detected by paper chromatography. For example, the benzyl and *sec*-butyl glucosinolates in *Thelypodium rollinsii* and the 4-methylthiobutyl glucosinolate and 5-methylthiopentyl glucosinolate in *T. laciniatum* were not detected by paper chromatography. Moreover, the isobutyl isothiocyanate was not detected by the paper-chromatographic analysis of its derived thiourea in all samples of *T. laciniatum* and

TABLE 5. GLUCOSINOLATES PRESENT IN THE GENUS THELYPODIUM*

Compound No.	Systematic Name	Side Chain, R
1	Isopropyl glucosinolate	$(CH_3)_2CH$–
2	2-Hydroxy-1-methylethyl glucosinolate	$HOCH_2CH(CH_3)$–
3	Isobutyl glucosinolate	$(CH_3)_2CHCH_2$–
4	*sec*-Butyl glucosinolate	$C_2H_5CH(CH_3)$–
5	1-(Hydroxymethyl) propyl glucosinolate	$C_2H_5CH(CH_2OH)$–
6	3-Methylthiopropyl glucosinolate	$CH_3S(CH_2)_3$–
7	Allyl glucosinolate	$H_2C{=}CHCH_2$–
8	4-Methylthiobutyl glucosinolate	$CH_3S(CH_2)_4$–
9	4-Methylsulfinylbutyl glucosinolate	$CH_3SO(CH_2)_4$–
10	4-Methylsulfonylbutyl glucosinolate	$CH_3SO_2(CH_2)_4$–
11	3-Butenyl glucosinolate	$H_2C{=}CH(CH_2)_2$–
12	2-Hydroxy-3-butenyl glucosinolate	$H_2C{=}CHCHOHCH_2$–
13	5-Methylthiopentyl glucosinolate	$CH_3S(CH_2)_5$–
14	5-Methylsulfinylpentyl glucosinolate	$CH_3SO(CH_2)_5$–
15	4-Pentenyl glucosinolate	$H_2C{=}CH(CH_2)_3$–
16	Benzyl glucosinolate	$C_6H_5CH_2$–
17	2-Phenylethyl glucosinolate	$C_6H_5(CH_2)_2$–

*Arranged according to Ettlinger and Kjaer (1968) with the addition of the recently discovered isobutyl glucosinolate (Underhill and Kirkland, 1972).

T. milleflorum. This failure is due to the fact that isobutylthiourea and *sec*-butylthiourea give similar R_{Ph} values, making it impossible to resolve them by paper chromatography (Kjaer and Rubinstein, 1953). Further comparison between the GLC and paper chromatography results show the superiority of the former approach for both qualitative and quantitative determinations. However, the latter approach is still very valuable, particularly in connection with the nonvolatile glucosinolate derivatives.

There is some variation in the glucosinolate composition between the basal leaves and the seeds of the same species (Table 6). The basal leaves of *Thelypodium wrightii* (Correll 34106), *T. repandum* (6921), and *T. laciniatum* (68133) contained small amounts of 5-methylsulfinylpentyl glucosinolate, which was not detected in the seeds of the same samples. Moreover, the leaves of *T. wrightii* showed a trace of the benzyl glucosinolate, which was not detected in the seeds, while the seeds contained 2-hydroxy-3-butenyl glucosinolate, which appeared to be lacking from the leaves. Qualitative variation in the glucosinolate contents of different parts of a given plant has been demonstrated by Gmelin and Kjaer (1970), Josefsson (1967), and Ettlinger and Kjaer (1968).

The R_{Ph} values of the thioureas and oxazolidine-2-thiones, as encountered in *Thelypodium*, hold good to $\pm$ 0.03 or $\pm$ 0.04 and rarely vary as much as $\pm$ 0.05. These values, as shown in Table 7, are only slightly different from those of Ettlinger and Thompson (1962 and unpublished). Most of the variability in the R_{Ph} values is probably caused by fluctuation in temperature.

The identification of the various isothiocyanates by GLC was always aided by injection of the isothiocyanate standards either separately or mixed with small proportions of the sample. This precaution was very necessary, because the retention time (the time from injection of the sample to the appearance of the top of the peak) of a given isothiocyanate was not always the same. The variation in the retention time was probably caused by slight differences in column temperature and flow rate of the carrier gas. The variability in retention time increases as the volatility of the isothiocyanate decreases (Table 8).

TABLE 6. PAPER CHROMATOGRAPHY RESULTS

Species	Collection No.	Plant part	Glucosinolate*
Thelypodium brachycarpum	6949	seed	(11), 14?
T. crispum	6939	"	(7), 8, 9, 10, (11), 13, 14?, 15
T. eucosmum	6972	"	(11)
T. flexuosum	6953	"	(12)
T. howellii ssp. spectabilis	6958	"	1, (11)
T. integrifolium ssp. affine	68128	leaf	(12)
	Lund-B	seed	(12)
ssp. complanatum	6926, 6934, 6954, 6956	"	(12)
ssp. gracilipes	6993, 6994	"	(12)
ssp. integrifolium	6967, 6973, 6974, 6977, 6995	"	(12)
ssp. longicarpum	6991	"	(12)
T. laciniatum	68152	"	4, (11), 15
	6970, 6971, 6968, 6965, 6963	"	1, 4, (11), 15
	6959, 6960	"	1, 4, (11), 15, 17
	68133	"	4, (11), 17
	"	leaf	4, (11), 14, 16, 17
T. milleflorum	68154, 68160, 6966	seed	(1), (4), 17
	6961, 6962, 6964		(1), (4), 16, 17
T. repandum	6921, Hitchcock 14120	"	(12)
	6921	leaf	(12), 14
T. rollinsii	6979, 6980, 6981, 6982, 6983	seed	(7), 11
T. sagittatum ssp. sagittatum	6919, 6925, 6929	"	(1), (2). 4. 5
ssp. ovalifolium	6984	"	(1), (2), 4, 5
T. stenopetalum	6947	"	(1), 4
T. texanum	Barclay 713, Cory 43996, Rollins 6176, Rollins 61106	"	(12)
T. wrightii	6992	"	(12)
	Correll 34106	"	(11), (12)
	" "	leaf	(11), 14, 16

*Numbers correspond to those in Table 5. Compounds in parentheses are primary, others secondary constituents.

TABLE 7. R_{Ph} VALUES OF THIOUREAS AND OXAZOLIDINE-2-THIONES*

Compound	Solvent Systems					
	But.	3-Tol.	10-Tol.	Chlor.	Benz.	Tol-Ac.
Isopropylthiourea	–	0.85	0.60	0.41	0.32	0.26
4-Methyloxazolidine-2-thione	–	0.84	0.82	0.91	0.95	0.69
sec-Butylthiourea	–	–	0.96	0.74	0.72	0.62
4-Ethyloxazolidine-2-thione	–	–	1.13	1.18	1.44	1.34
Allylthiourea	–	0.78	0.45	0.25	0.25	0.18
4-Methylthiobutylthiourea	–	–	1.12	0.96	1.02	0.82
4-Methylsulfinylbutylthiourea	0.42	0.08	0.0	0.0	0.0	0.0
4-Methylsulfonylbutylthiourea	0.54	0.15	0.03	0.03	0.0	0.0
3-Butenylthiourea	–	–	0.83	0.60	0.58	0.43
5-Vinyloxazoldine-2-thione	–	–	1.07	1.09	1.33	1.10
5-Methylthiopentylthiourea	–	–	1.28	1.12	1.41	1.23
5-Methylsulfinylpentylthiourea	0.56	0.17	0.03	0.02	0.0	0.0
4-Pentenylthiourea	–	–	1.15	0.90	1.02	0.88
Benzylthiourea	–	–	1.18	0.92	1.11	0.82
2-Phenylethylthiourea	–	–	1.29	1.07	1.41	1.24

*Compounds arranged according to Table 5.
Solvent Systems: But. = 1:3:1 toluene-butyl alcohol-water; 3-Tol. = 3:1:2 toluene-butyl alcohol-water; 10-Tol. = 10:1:2 toluene-butyl alcohol-water; Chlor. = 5:3 chloroform-water; Benz. = 5:1:2 benzene-ethanol-water; Tol-Ac. = 5:2:4 toluene-acetic acid-water.

TABLE 8. RETENTION TIMES OF SOME ISOTHIOCYANATES

Isothiocyanate	Retention time		Approximate range of variation (± seconds)
	Minutes	Seconds	
Group I			
Isopropyl isothiocyanate	2	06	6
Allyl isothiocyanate	2	57	12
sec-Butyl isothiocyanate	3	44	12
Isobutyl isothiocyanate	4	19	14
3-Butenyl isothiocyanate	5	39	25
4-Pentenyl isothiocyanate	10	45	45
Group II			
3-Methylthiopropyl isothiocyanate	2	57	8
Benzyl isothiocyanate	3	45	15
4-Methylthiobutyl isothiocyanate	4	55	17
2-Phenylethyl isothiocyanate	5	57	22
5-Methylthiopentyl isothiocyanate	8	02	32

Group I was characterized at 80°C, group II at 160°C.

Two unknown volatile compounds were detected in the GLC analyses of seed samples of certain species of *Thelypodium*. One of them was present in very small quantities in some of the samples of *T. wrightii*, *T. laxiflorum*, and *T. integrifolium*. This compound is probably a cyanide derivative, but no attempt has been made to characterize it. The second unknown was sometimes present in concentrations close to 11% of the total volatile content, but was only found in the species that had high concentrations of 3-butenyl isothiocyanate (Table 15, compound 11). This compound is probably 3-butenyl cyanide (Dr. Martin G. Ettlinger, personal communication). Neither of the unknowns were included in the quantifications of the volatile isothiocyanate contents and will not be mentioned in the rest of the discussion.

In the following, the terms isothiocyanate and glucosinolate are occasionally used interchangeably. However, it should be remembered that the isothiocyanates are the hydrolysis products of the glucosinolates.

Thelypodium laciniatum is the most varied chemically of all the species of the genus. Five to nine glucosinolates have been identified in the seeds of each of the various population samples of this species. The major isothiocyanate-producing glucoside in this species is 3-butenyl glucosinolate (Table 9). It tends to be present in slightly higher concentrations in the populations of Oregon and Washington than in those of Idaho or California. The second significant component, which has also been found in all the population samples of this species, is *sec*-butyl glucosinolate (Table 9). The 4-pentenyl glucosinolate was a minor constituent in all the population samples but the three from Idaho. These three samples were collected from the central portion of the state, which is the eastern-most limit of the species range. The isopropyl glucosinolate was found in small amounts in all the samples but those from Idaho. Instead, the three from Idaho had traces of the allyl glucosinolate, which was not detected in the other samples of the species. The amounts of 4-pentenyl glucosinolate in the Idaho samples were higher than anywhere else in the genus. The isobutyl glucosinolate was present in very small quantities in *T. laciniatum* as compared to its concentrations in the closely related *T. milleflorum*. The benzyl, 4-methylthiobutyl, and 5-methylthiopentyl glucosinolates were present either alone or in various combinations, but always in small quantities. They were not detected in some of the samples (Table 9). The distribution of these three glucosinolates does not seem to offer any recognizable pattern. Substantial amounts of 2-phenylethyl glucosinolate occurred in the three population samples from California.

In *Thelypodium milleflorum* isopropyl and *sec*-butyl glucosinolates were the major constituents in all the samples analyzed. The first glucosinolate was the dominant compound in most of the samples, particularly those from the state of Washington (Table 10). However, in samples

TABLE 9. ISOTHIOCYANATES OF THELYPODIUM LACINIATUM (%)

Collection No.	State	$(CH_3)_2CHNCS$	$H_2C{=}CHCH_2NCS$	$C_2H_5CH(CH_3)NCS$	$(CH_3)_2CHCH_2NCS$	$H_3C{=}CH(CH_2)_2NCS$	$H_3C{=}CH(CH_2)_3NCS$	$C_6H_5CH_2NCS$	$CH_3S(CH_2)_4NCS$	$C_6H_5(CH_2)_2NCS$	$CH_3S(CH_2)_5NCS$
68132	California	T	0	17.9	T	61.1	T	0.8	3.0	15.7	1.5
68133	"	1.3	0	14.2	T	64.7	2.2	0.6	4.5	9.9	2.6
6951	"	T	0	14.0	T	71.4	2.1	T	4.7	7.8	T
6922	Idaho	0	T	8.0	T	67.6	24.4	T	0	0	0
6923	"	0	T	8.5	T	68.3	23.3	0	0	0	0
6924	"	0	T	12.5	T	58.4	29.1	0	0	0	0
68145	Oregon	T	0	17.4	T	79.2	T	0	3.4	0	0
6955	"	2.4	0	17.7	T	78.0	1.9	0	0	0	0
6959	"	T	0	15.5	T	77.4	3.0	0	2.1	2.0	0
6960	"	1.1	0	26.0	T	66.1	2.4	0.6	2.2	1.6	T
6970	"	T	0	19.0	T	76.2	3.4	0	1.4	T	0
6971	"	T	0	15.5	T	82.3	2.2	0	0	0	0
Howell 1880	"	1.7	0	8.3	T	89.3	T	T	0	0.7	0
6963	Washington	T	0	10.0	T	79.0	2.0	1.2	2.9	3.5	1.4
6965	"	T	0	14.7	T	79.1	2.5	T	3.7	T	0
6968	"	T	0	7.5	T	88.8	1.1	T	2.6	T	0

T = trace, 0 = undetected

68154 and 68160 from Idaho and sample 2540 that was collected by Rollins and Chambers in Nevada, the concentration of the *sec*-butyl glucosinolate was slightly to moderately higher. Benzyl and 2-phenylethyl glucosinolates were both present in minor amounts, with more of the latter than the former.

Isobutyl isothiocyanate has been recently reported by Underhill and Kirkland (1972) from the fresh parts of the crucifer *Conringia orientalis* (L.) Andrz. As found earlier by Kjaer *et al.* (1956), this compound is absent from the seeds. We now know that it is present in the seeds of two species of *Thelypodium* (*T. laciniatum* and *T. milleflorum*) and *Cochlearia officinalis* (Ettlinger and Al-Shehbaz, unpublished). Isobutyl isothiocyanate was a minor compound in all the samples of *Thelypodium milleflorum* but the concentrations were clearly higher than those seen in *T. laciniatum* (Tables 9 and 10).

In his treatment of the genus *Thelypodium*, Payson (1923) recognized three varieties in *T. laciniatum*. These are vars. *laciniatum*, *milleflorum*, and *streptanthoides*. In the present treatment, however, var. *milleflorum* is considered a distinct species, while var. *streptanthoides* is not given any taxonomic recognition. Chemically, the two species are

TABLE 10. ISOTHIOCYANATES OF THELYPODIUM MILLEFLORUM (%)

Collection number	State	$(CH_3)_2CHNCS$	$C_2H_5CH(CH_3)NCS$	$(CH_3)_2CHCH_2NCS$	$H_2C{=}CH(CH_2)_2NCS$	$C_6H_5CH_2NCS$	$C_6H_5(CH_2)_2NCS$
68154	Idaho	38.0	50.7	8.3	0	T	3.0
68160	"	40.1	47.2	7.5	1.5	T	3.7
Palmer 417	"	58.3	36.7	5.0	0	T	T
6933	Nevada	53.7	32.0	5.6	0	0.8	7.9
Rollins & Chambers 2540	"	35.8	57.5	6.7	0	T	T
68140	Oregon	61.6	20.6	4.8	0	T	13.0
6961	Washington	82.4	12.0	4.7	0	T	0.9
6962	"	84.0	12.0	2.4	0	0.6	1.0
6964	"	78.7	15.8	4.5	0	T	1.0
6966	"	73.1	20.1	3.4	0	T	3.4
St. John 7650	"	63.6	34.8	1.5	0	0	0

T = trace, 0 = undetected

very distinct in a number of ways. *Thelypodium laciniatum* is characterized by having high concentrations of 3-butenyl glucosinolate, low to moderate amounts of the *sec*-butyl glucosinolate, traces or none of isopropyl glucosinolate, low to moderate amounts of 4-pentenyl glucosinolate, and bare traces of isobutyl glucosinolate (Table 9 and Plate 16). *Thelypodium milleflorum*, on the other hand, has high concentrations of isopropyl glucosinolate, and high to moderate amounts of *sec*-butyl glucosinolate. Measurable amounts of isobutyl glucosinolates were always present, but no detectable quantities of 4-pentenyl and 3-butenyl glucosinolates were found in any of the samples (except 68160 which needs further checking). Such significant differences in the chemistry clearly favor the maintenance of these two taxa as distinct species (Table 10 and Plate 16).

In one locality (near Beverly, Washington) where they were growing near each other, *Thelypodium laciniatum* and *T. milleflorum* were as distinct chemically as they were elsewhere in their ranges (sample 6963 in Table 9 and sample 6962 in Table 10). Neither chemical nor morphological intermediates were found. It is clear that genetic isolation is present between the two species in nature.

Variety *streptanthoides* was based mainly on the differences in flower color. However, this character does not seem to have any significance in the genus. Five samples (6959, 6960, 6965, 6968, and 6970 in Table 9) of *Thelypodium laciniatum* that clearly fall in var. *streptanthoides sensu*

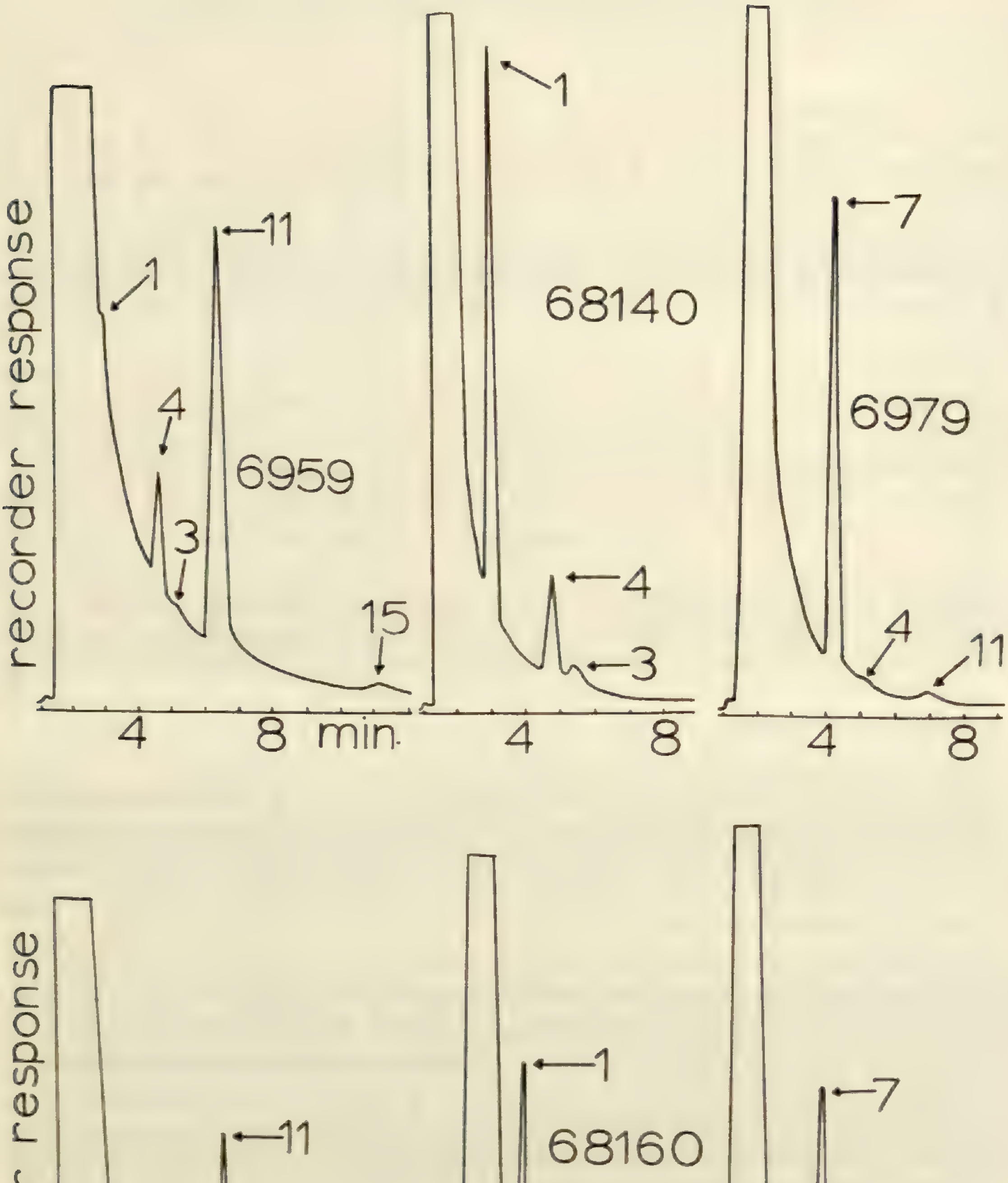


PLATE 16. Chromatographic tracings of isothiocyanates of *Thelypodium laciniatum* (6959, 6923), *T. milleflorum* (68140, 68160), and *T. rollinsii* (6979, 6982). 2 μl injected at 80° C. Numbers 1, 3, 4, 7, 11, and 15 are the isothiocyanates derived from their respective glucosinolates in Table 5.

Payson are chemically indistinguishable from other samples of this species as far as the pattern of their glucosinolate distribution is concerned.

It is clearly shown that the glucosinolates are very stable compounds by the comparison of the recently collected samples with much older ones obtained from herbarium specimens, such as those collected by Howell and Palmer in the years 1880 and 1895 respectively (Tables 9 and 10).

One of the taxonomically most confused groups of taxa in *Thelypodium* is the *T. integrifolium* complex. As many as six species were described in this group. Payson (1923) recognized six taxa, including four species and two varieties. In the present treatment one species and five subspecies are recognized. *Thelypodium rollinsii*, a new species added to this complex, differs in many significant morphological features from *T. integrifolium*. The glucosinolate distribution agrees well with the taxonomic decisions. All of the subspecies of *T. integrifolium* have one major glucoside, 2-hydroxy-3-butenylglucosinolate. No volatile isothiocyanates have been detected in this species (Table 6).

Thelypodium rollinsii has a completely different pattern of glucosinolates (Plate 16) from that of the closely related *T. integrifolium*. The major isothiocyanate-producing glucoside in this species is allyl glucosinolate, forming over 70% of the total. Small amounts of 3-butenyl glucosinolate were found in the three samples from Juab County, but significantly higher concentrations were present in samples 6982 and 6983, collected from two other counties of Utah, Sanpete, and Sevier respectively (Table 11). These two samples contained slightly smaller amounts of allyl glucosinolate than the other three. Other differences are present (Tables 6 and 11) but it is clear that we are dealing with two significantly different patterns of glucosinolates that justify, from the chemical point of view, the recognition of two distinct species.

Thelypodium laxiflorum has been considered a variety of *T. wrightii* under the name *tenellum* since 1895. However, the two taxa are so extremely different in their flower and fruit morphology (see the taxonomic treatment and Plate 22) that they are best treated as distinct species. The major compound in *T. wrightii* is 2-hydroxy-3-butenyl glucosinolate. This was not detected in *T. laxiflorum* (Table 12). The 3-butenyl isothiocyanate was found in measurable amounts in sample 34106 but not in 6992. This compound was the major mustard oil in *T. laxiflorum*, constituting more than 80% of the total isothiocynate content in the seeds (Table 12). The remainder included small amounts of isopropyl, allyl, *sec*-butyl, 4–pentenyl, benzyl, 4-methylthiobutyl, and 5-methylthiopentyl isothiocyanates, none of which were detected in *T. wrightii*. Unfortunately, we are dealing with a very few samples which may not reflect the main variability in the two species. Nevertheless, the two species appear to have two distinct patterns in their glucosinolates which is solid evidence against uniting them in a single species.

TABLE 11. ISOTHIOCYANATES OF THELYPODIUM ROLLINSII (%)

Collection number	County in Utah	$H_2C=CHCH_2NCS$	$C_2H_5CH(CH_3)NCS$	$H_2C=CH(CH_2)_2NCS$	$C_6H_5CH_2NCS$
6979	Juab	93.9	T	4.4	1.7
6980	"	95.2	T	3.8	1.0
6981	"	94.5	T	4.1	1.4
6982	Sanpete	74.1	T	24.7	1.2
6983	Sevier	73.6	T	25.3	1.1

T = trace

TABLE 12. ISOTHIOCYANATES OF THELYPODIUM LAXIFLORUM (%)

Collection number	State	$(CH_3)_2CHNCS$	$H_2C=CHCH_2NCS$	$C_2H_5CH(CH_3)NCS$	$H_2C=CH(CH_2)_2NCS$	$H_2C=CH(CH_2)_3NCS$	$C_6H_5CH_2NCS$	$CH_3S(CH_2)_4NCS$	$C_6H_5(CH_2)_2NCS$	$CH_3S(CH_2)_5NCS$
6985	Utah	3.3	0	1.4	88.9	4.7	0.7	0.5	0.5	T
Lund-A	Utah	T	T	T	93.4	4.6	0.6	0.7	T	0.7
Beatley 9426	Nevada	T	T	2.1	92.1	2.7	0.4	0.6	0.5	1.6

T = trace, 0 = undetected

TABLE 13. ISOTHIOCYANATES OF THELYPODIUM SAGITTATUM (%)

Collection number	State	$(CH_3)_2CHNCS$	$C_2H_5CH(CH_3)NCS$	$C_6H_5CH_2NCS$	$C_6H_5(CH_2)_2NCS$
subsp. ovalifolium					
6984	Utah	85.5	14.5	T	T
subsp. sagittatum					
6915	Utah	72.8	27.2	0	0
6919	Idaho	81.5	18.5	0	0
6925	Nevada	76.6	23.4	0	0
6929	Nevada	82.4	17.6	0	0

T = trace, 0 = undetected

The treatment of the *Thelypodium sagittatum* complex by Payson (1923) included two species and a variety, namely *T. ovalifolium, T. sagittatum,* and *T. sagittatum* var. *crassicarpum.* In the present treatment, var. *crassicarpum* is recognized as a distinct species named *T. paniculatum,* while *T. ovalifolium* is reduced to subspecific rank under the widely distributed *T. sagittatum.* The two subspecies of *T. sagittatum* are almost indistinguishable in their glucosinolate contents (Tables 6 and 13). The major glucoside is isopropyl glucosinolate, representing more than 70% of the total content of isothiocyanate-producing glucosides. The *sec*-butyl glucosinolate was a minor constituent in both subspecies, but was present in moderate amounts. Two additional compounds were present in very small amounts in subsp. *ovalifolium* and were identified as benzyl and 2-phenylethyl glucosinolates. In addition to these, 2-hydroxy-1-methylethyl glucosinolate and 1-(hydroxymethyl)propyl glucosinolate were present. Upon hydrolysis, they give rise to 4-methyloxazolidine-2-thione and 4-ethyloxazolidine-2-thione respectively. These two glucosinolates were first discovered in the seeds of *Sisymbrium austriacum* Jacq. by Kjaer and Christensen (1959, 1962). That these two glucosinolates are not found in any other members of the genus *Thelypodium* except *ovalifolium* and *sagittatum,* plus the overall similarities in the glucosinolate contents of these two taxa clearly supports their treatment taxonomically as a single species. *Thelypodium paniculatum* is very distinct from *T. sagittatum* (Table 14).

The two samples of *Thelypodium howellii* subsp. *spectabilis* analyzed were significantly different from each other. In sample 6957 the predomi-

TABLE 14. ISOTHIOCYANATES OF CERTAIN SPECIES OF THELYPODIUM (%)

Species	Collection number	State	$(CH_3)_2CHNCS$	$H_2C{=}CHCH_2NCS$	$C_6H_5CH(CH_3)NCS$	$H_2C{=}CH(CH_2)_4NCS$	$H_2C{=}CH(CH_2)_3NCS$	$CH_3S(CH_2)_4NCS$	$C_6H_5CH_2CH_2NCS$	$CH_3S(CH_2)_4NCS$	$C_6H_5(CH_2)_2NCS$	$CH_3S(CH_2)_5NCS$
T. howellii	6957	Oregon	96.3	0	0	T	0	3.7	T	0	0	0
	6958	"	7.7	0	0	92.3	T	0	T	0	0	0
T. eucosmum	6972	"	T	6.3	1.1	90.9	0.7	0	T	1.0	0	0
T. paniculatum	6976	Wyoming	T	6.9	0.8	89.5	2.8	0	0	0	0	0
T. stenopetalum	6947	California	89.6	0	10.4	0	0	0	T	0	T	0
T. brachycarpum	6949	"	0	1.7	1.1	97.2	0	0	0	0	0	0
	6952	"	0	59.2	0	40.8	0	0	T	0	0	0
T. crispum	6939	Nevada	0	23.7	0	64.7	4.2	0	T	3.7	0	3.7
	6942	California	0	2.9	1.7	87.7	4.5	0	0.5	1.8	0	0.9
	6943	"	0	2.0	1.0	91.0	2.6	0	T	2.1	0	1.3

T = trace, 0 = undetected

nant compound was the isopropyl glucosinolate, while in sample 6958 the major compound was 3-butenyl glucosinolate. Other differences were minor (Table 14). The two samples were collected from the extreme southern and northern portions of the subspecies range respectively. Significant geographic variation in the glucosinolate contents of one species or subspecies has been found in *Brassica juncea* (L.) Czern. by Hemingway *et al.* (1961), Vaughan *et al.* (1963), and Vaughan and Gordon (1973) as well as in certain taxa of the genus *Cakile* (Rodman, personal communication).

Thelypodium stenopetalum resembles both *T. milleflorum* and *T. sagittatum* subsp. *ovalifolium* in its volatile isothiocyanate, but differs from the former in lacking the isobutyl isothiocyanate and from the latter in having no oxazolidine-2-thiones. However, the three species are not morphologically related. The remaining species in Table 14 (*T. eucosmum*, *T. paniculatum*, *T. brachycarpum*, and *T. crispum*) are similar to each other in having high concentrations of 3-butenyl isothiocyanate as well as detectable amounts of allyl isothiocyanate. However, it is not safe to make generalizations from such a limited number of samples. *Thelypodium brachycarpum* seems to lack 4-pentenyl, 4-methylthiobutyl, and 5-methylthiopentyl glucosinolates that were present in small amounts in *T. crispum*. These differences probably have some chemotaxonomic value.

Thelypodium texanum was said to have an oxazolidine-2-thione as the major constituent of the seeds as well as small amounts of a volatile isothiocyanate (Daxenbichler *et al.* 1964—*Stanleyella texana* in their account). In the present treatment, five samples of *T. texanum* were analyzed (Barclay 713, Cory 43996, Johnston 5263, Rollins 6176, and Rollins 61106). All five samples had 2-hydroxy-3-butenyl glucosinolate as the sole glucoside, and no traces of any volatile isothiocyanates were detected. These results are in agreement with those obtained earlier by Ettlinger and Thompson (personal communication) from another sample of the same species. Whether the sample analyzed by Daxenbichler *et al.* (1964) did contain a volatile isothiocyanate or not is still an open question.

The sole glucoside in the seeds of *Thelypodium flexuosum* (sample 6953) and *T. repandum* (6921 and Hitchcock 14120) is 2-hydroxy-3-butenyl glucosinolate. Three of the five species (*T. wrightii*, *T. texanum*, and *T. repandum*) that had this glucosinolate as the major or sole constituent are somewhat related to each other. The other two species, *T. integrifolium* and *T. flexuosum*, are not related to each other or the other three species. This is the only group of species in which the glucosinolate distributional patterns clearly are not species-specific.

The distributional patterns of the glucosinolates in the various species of *Thelypodium* are summarized in Table 15. This table includes the results from paper chromatography as well as the GLC results from seed samples. Any given sample may or may not have all the glucosinolates

listed under the species to which it belongs. Certain species have as many as 10 kinds of glucosinolates, while others have as few as one. These patterns are undoubtedly genetically controlled, but we have no idea as to why natural selection favors the presence of one glucosinolate in certain taxa and several or many in others.

TABLE 15. SEED GLUCOSINOLATES OF THELYPODIUM

Taxon	Glucosinolates*
T. brachycarpum	4, (7), (11), 14?, 16
T. crispum	4, 7, 8, 9, 10, (11), 13, 14?, 15, 16
T. eucosmum	1, 4, 7, 8, (11), 15, 16
T. flexuosum	(12)
T. howelli ssp. spectabilis	(1), 6, (11), 15, 16
T. integrifolium (all 5 sspp.)	(12)
T. laciniatum	1, 3, 4, 7, 8, (11), 13, 15, 16, 17
T. laxiflorum	1, 4, 7, 8, (11), 13, 15, 16, 17
T. milleflorum	(1), 3, (4), 16, 17
T. paniculatum	1, 4, 7, (11), 15
T. repandum	(12)
T. rollinsii	4, (7), 11, 16
T. sagittatum ssp. sagittatum	(1), (2), 4, 5
ssp. ovalifolium	(1), (2), 4, 5, 16, 17
T. stenopetalum	(1), 4, 16, 17
T. texanum	(12)
T. wrightii ssp. wrightii	(11), (12)

*Numbers refer to glucosinolates in Table 5.
Numbers in parentheses are the dominant glucosides in the species

Systematic and evolutionary considerations. With the exception of a few species, the quantitative as well as the qualitative patterns of glucosinolates in *Thelypodium* (Table 15) were by and large species-specific. The exceptions are the five species with the 2-hydroxy-3-butenyl glucosinolate (compound no. 12) and *T. eucosmum* and *T. paniculatum* that are probably chemically indistinguishable. As far as the intrapopulational variability of the glucosinolates is concerned, some quantitative and almost no qualitative differences have been found between the plants of a given population. However, very few samples have been analyzed in this connection, and the possibility of finding qualitative differences within the same population is not excluded.

The question of how much the chemical data can contribute to our knowledge of the evolutionary or "phylogenetic" relationships between taxa or various categorical levels is an interesting one. The chemistry of the "secondary" compounds appears to have limited implications when used as a criterion of evolutionary relationships above the genus level (Alston, 1967). Turner (1969) pointed out that such micromolecular data are mainly useful on the genus level or below. As far as the gluco-

sinolates are concerned, they do not seem to provide major help, at present, to our knowledge of the tribal, subtribal, and generic classifications within the family Cruciferae. However, this may be in part a reflection of the lack of chemical data from the majority of genera of the family, and the lack of an adequate tribal classification. The six genera investigated belonging to the tribe Thelypodieae (*Stanleya*, *Thelypodium*, *Thelypodiopsis*, *Caulanthus*, *Streptanthus*, and *Streptanthella*) showed no distinct patterns in their glucosinolate distribution that set them apart. However, some species of the genera *Caulanthus* and *Streptanthus* showed higher concentrations of certain glucosinolates that were either lacking or present in very small quantities in the other four genera. The results from the five genera other than *Thelypodium* will be published in a separate paper. It is not surprising to find a few examples where the mustard oils offer some help in establishing lines between closely related genera with confused boundaries. For example, controversy still exists as to whether *Sinapis* should be merged with *Brassica* or maintained as a distinct genus. The two species of *Sinapis* that have been investigated for their mustard oils have *p*-hydroxybenzyl glucosinolate, which has not been detected in the cultivated species of *Brassica*. Furthermore, species of the latter genus contain methionine-derived glucosinolates that are lacking in *Sinapis* (Ettlinger and Thompson, 1962; Ettlinger, personal communication). Such significant differences in the chemistry add to the justification of maintaining the two genera as distinct. The glucosinolates are probably most useful in the study of species belonging to one genus both on the inter- and intraspecific levels.

In conclusion, we can safely say that the glucosinolates provide valuable information to systematists working with the family Cruciferae and probably other families that contain them. Their distributional patterns in *Thelypodium* were shown to provide support for a number of taxonomic decisions reached in the present treatment. This is particularly true when it comes to maintaining *T. laciniatum* and *T. milleflorum* as distinct species instead of varieties of one species. The same is true for *T. wrightii* and *T. laxiflorum*. Also, the patterns are in agreement with other decisions reached in the *T. integrifolium* and *T. sagittatum* complexes, which have had a long history of confused taxonomy.

Evolution within the Genus

In the study of evolutionary relationships or trends between species of a single genus, the synthetic approach, combining data from cytology, palynology, chemistry, anatomy, and morphology, undoubtedly leads to a better understanding of the taxa involved than a single approach. However, it is unfortunate that the cytology, palynology, and chemistry offer very little help, if any, to our understanding of the evolutionary relationships between species of *Thelypodium*. Therefore, the following

discussion is based primarily on the various morphological aspects of the species involved.

As suggested by Payson (1923) and Rollins (1939), *Thelypodium* is more closely related to *Stanleya* than to any other genus placed here in the tribe Thelypodieae. Taking the various morphological aspects into consideration, one encounters no major difficulties in deciding which species are most primitive and which are advanced.

The 18 species of *Thelypodium* recognized in the present treatment may easily be divided into three major groups, each of which is made up of interrelated species. The groups are named after their oldest described species and they are: the *T. laciniatum*, *T. sagittatum*, and *T. wrightii* groups. The first group contains *T. laciniatum* and *T. milleflorum*. It has more primitive features than either of the others and yet it ties in with both of them by certain morphological characters. For example, it resembles the *T. wrightii* group in having somewhat flattened siliques, filaments that are exserted and nearly equal in length (*T. laxiflorum* is an exception), petioled cauline leaves, and a continuous mold of glandular tissue, but it differs by its long and densely-flowered racemes, erect floral parts, larger flowers, and petals that are differentiated into distinct deltoid-lanceolate claws and long, narrow blades. In the *T. wrightii* group, the inflorescence is mostly corymbose, the floral parts are spreading (except in *T. laxiflorum*), and the petals are hardly differentiated into claws and blades, but when they are so, the claws are very short and not flattened. The most important characters distinguishing the *T. sagittatum* group from the other two are the sessile and mostly amplexicaul to auriculate cauline leaves and the terete siliques that characterize all its species.

Within the *Thelypodium laciniatum* group, *T. milleflorum* appears to be more advanced and probably had its origin from an ancestor not far from *T. laciniatum*. It is rather difficult to tie the species of this group directly with those of the other two. This is probably because of the considerable morphological discontinuities between them. Although it is not difficult to imagine the possible derivation of the *T. sagittatum* group from an ancestor not far from the *T. laciniatum* group, it is much harder to speculate about the relationship between the *T. laciniatum* and *T. wrightii* groups because of the marked dissimilarities in their flowers. However, it seems that the latter is more advanced than the former, because of its smaller flowers, corymbose inflorescences, and obsolete gynophores (a few exceptions do exist). There is probably no close relationship between the *T. wrightii* and *T. sagittatum* groups.

The *Thelypodium wrightii* group is made up of six species that are sharply defined and somewhat related to each other. *Thelypodium laxiflorum* is the only species of the group with erect floral parts (sepals sometimes spreading) and terete siliques. However, it is more related to *T. wrightii* than to any other species of the genus. *Thelypodium laxi-*

florum is probably advanced within the group, because of its siliques and tetradynamous stamens. *Thelypodium paysonii* is somewhat isolated because of its pubescent claws and filaments and the non-torulose siliques. It might represent a separate line from a remote ancestor of the group. *Thelypodium texanum* and *T. tenue* are very closely related to each other. It is likely that the latter species had its origin from the former.

The remaining ten species of the genus constitute the well-defined *Thelypodium sagittatum* group. Three species here, *T. crispum, T. brachycarpum,* and *T. eucosmum,* are more closely related to each other than to the other seven. They are somewhat intermediate morphologically between the *T. laciniatum* group and the remainder of the *T. sagittatum* group, because of their densely flowered inflorescences (they occasionally show lax racemes), long and exserted filaments that are nearly equal in length, and petals that are differentiated into claw and blade. Perhaps the remaining species had their origin from ancestors not significantly different from these three species. The most advanced species in this group appear to be *T. sagittatum, T. paniculatum,* and *T. flexuosum.* They have corymbose inflorescences (*T. sagitattum* is sometimes an exception), tetradynamous stamens that are included, petals that are somewhat undifferentiated into blade and claw, and anthers that are short and rarely coiled when dehisced. The three species are related, but they do not appear to be directly linked to each other. More likely, they have had an independent origin from a common ancestor. Two species in the *T. sagittatum* group, *T. rollinsii* and *T. integrifolium,* are fairly different from the rest in having totally glabrous basal leaves and sessile to minutely auriculate cauline leaves. *Thelypodium integrifolium* appears to be more advanced than *T. rollinsii,* because it has sessile, non-auriculate cauline leaves (not found elsewhere in the genus) and highly evolved nectar glands, while the latter species has distinctly auriculate leaves and a continuous mold of glandular tissue. Both of these features are found in some of the primitive members of the group. Therefore, *T. rollinsii* is somewhat intermediate between *T. integrifolium* and some species of the *T. sagittatum* group.

Evolutionary Trends within Thelypodieae

The ten genera of the tribe Thelypodieae seem to fall into three groups according to the degree of primitiveness or advancement in their overall flower and fruit morphology. *Stanleya* and *Warea* are probably the least specialized of the tribe. Some of the features considered to be primitive in these genera are: long and exserted filaments that are equal in length; long and coiled anthers; densely-flowered inflorescences; sessile stigmas; and, usually long gynophores. These are some of the important features that are shared by the two genera and some members of the subfamily Cleomoideae-Capparaceae. It is not surprising, therefore, that the first

species discovered in both *Stanleya* and *Warea* were described as *Cleome*. The three streptanthoid genera, *Streptanthus*, *Caulanthus*, and *Streptanthella*, probably represent the most advanced group in the tribe. This is particularly true as far as their flowers and siliques are concerned. The remaining five genera fall in an intermediate group between the streptanthoid and the stanleyoid groups. *Thelypodium* shows, rather clearly, various degrees of transition from the primitive that overlaps to a certain extent with the stanleyoid group to higher degrees of advancement that are found in some of the streptanthoid members. It is not suggested here that *Thelypodium* represents the link between the two groups. Rather, it is an ideal example for the study of the evolutionary trends that took the direction from the stanleyoid to the streptanthoid groups.

Payson (1923) presented a discussion on some of the trends he found in certain characters within *Thelypodium* and *Caulanthus*. Few of these trends are recognized here, while others, such as flower color, pubescence, and the nature of cauline leaves, are hard to visualize as to what direction they took. Some of the trends mentioned are similar to those summarized by Dvořàk (1971b) for the tribes Hesperideae and Sisymbrieae, while others seem to have taken the reverse direction. It is obvious that the evolutionary trends presented below are applicable to

TABLE 16. EVOLUTIONARY TRENDS IN THE THELYPODIEAE

Primitive	Advanced
1. Inflorescence densely flowered	inflorescence lax
2. Inflorescence racemose	inflorescence corymbose
3. Flowers actinomorphic	flowers zygomorphic
4. Floral parts spreading	floral parts erect
5. Sepals equal at base	sepals unequal at base, saccate
6. Petals differentiated into claw and blade	petals undifferentiated
7. Petals entire	petals crisped or chanelled
8. Stamens exserted	stamens included
9. Filaments equal in length	filaments tetradynamous or in three pairs of unequal length
10. Paired filaments free	paired filaments united
11. Anthers long and linear	anthers short and oblong or ovate
12. Anthers strongly coiled when dehisced	anthers straight or curved
13. Glandular tissue low, ring-like, subtending base of filaments and mostly surrounding base of single stamens	median tissue absent, or glands tooth-like
14. Fruiting pedicles horizontal, more or less straight	fruiting pedicels variously oriented or strongly curved
15. Siliques with long gynophores	siliques sessile or subsessile
16. Styles obsolete or absent	styles present
17. Stigmas entire	stigmas variously bilobed
18. Siliques slightly flattened or subterete	siliques strongly flattened or terete
19. Seeds wingless	seeds winged

most genera of the tribe, but some of them had probably taken the reverse direction in a few instances. These trends are summarized in Table 16.

It is probable that the evolutionary trends in the flowers and the inflorescences, presented in Table 16, did not take place independently. Any trends in these structures are very likely tied up directly or indirectly to the breeding system and the kind and behavior of the pollinating agent. For example, it is quite possible that inflorescences with numerous flowers, long and exserted anthers that produce large amounts of pollen, and filaments equal in length, are adaptations to attract pollen-collecting insects. On the other hand, showy flowers, short and tetradynamous filaments, small and included anthers, well-developed lateral glands, saccate lateral sepals, and few-flowered racemose or corymbose inflorescences might have evolved as an adaptation to attract nectar-sucking insects. Therefore, it does not seem unlikely that the evolutionary trends in the flowers and inflorescences of the Thelypodieae have resulted from the process of adaptation to different pollinators, such as a shift from pollen-collecting insects to nectar-sucking insects. The trends in the inflorescence may not always be connected to the pollinators. As suggested by Stebbins (1967), few-flowered inflorescences may have a selective advantage over the many-flowered ones in the areas where the flowering season or the growth season is short.

Thirteen of the trends listed in Table 16 have been detected within *Thelypodium* and these are all but numbers 3, 4, 16, 17, and 19. Zygomorphy is only known in the streptanthoid genera, but it is most pronounced in *Streptanthus* (Rollins, 1963b). It is hard to visualize whether the floral parts, because of their spreading nature, are primitive or advanced in *Thelypodium*, since this feature is present in species that are somewhat advanced on other morphological grounds. On the other hand, the spreading nature of floral parts in *Caulanthus anceps* is probably advanced, since this feature is very rare in the genus and the species is probably advanced in other respects (Payson, 1923, p. 252). The petals in the three streptanthoid genera are unique in having broad claws that are usually obovate to oblanceolate and blades that are often narrow and crisped or chanelled. However, a few exceptions do exist. Although we have indicated that the differentiated petals are more primitive than undifferentiated ones, they are probably advanced in the streptanthoid genera even though they are markedly differentiated into blades and claws. This is because of their unique morphology, which is probably very rare elsewhere in the Cruciferae.

It is clear that as a character, the length of the gynophore is very variable. Payson (1923) overemphasized the importance of gynophore length and considered it as a marker for the degree of primitiveness. In his thinking, the longer the gynophore the more primitive the species. How-

ever, the character can be quite variable within the same population (Plate 8) and in *Thelypodiopsis ambigua* it is found to vary from 0.1 to 1.5 centimeters. Distinct gynophores are found in the genera *Cardamine*, *Diplotaxis*, *Brassica*, and *Lunaria* and in the last genus they sometimes exceed three centimeters in length, but the genera are clearly advanced and not related to members of the Thelypodieae.

It is not possible to find any strong evidence to support the claim that incumbent cotyledons are more primitive than the accumbent ones. Both types are found within *Stanleya* and they are obliquely accumbent in *Warea*, while in *Thelypodium* they are obliquely accumbent to obliquely incumbent.

Some of the trends discussed here have probably taken the same direction in other tribes of the Cruciferae, while others have taken an opposite direction. A primitive feature within the Thelypodieae does not have to be so elsewhere in the family and this is probably true for the derived characters.

TAXONOMY

Thelypodium Endlicher, Genera Plantarum 876. 1839.

Type species: *Thelypodium laciniatum* (Hook.) Endl., in Walp. Repert. 1:172. 1842. Based on *Macropodium laciniatum* Hook., Bot. Miscell. 1:341. 1830.

Pachypodium Nutt. in Torr. & Gray, Fl. N. Am. 1:96. 1838, not *Pachypodium* Lindl. (1830), not *Pachypodium* Webb and Berth. (1836). Type species: *P. laciniatum* (Hook.) Nutt. Based on *Macropodium laciniatum* Hook.

Pleurophragma Rydb., Bull. Torr. Bot. Club 34:433. 1907. Type species: *P. integrifolium* (Nutt.) Rydb. Based on *Pachypodium integrifolium* Nutt.

Stanleyella Rydb., Bull. Torr. Bot. Club 34:435. 1907. Type species: *S. wrightii* (Gray) Rydb. Based on *Thelypodium wrightii* Gray.

Plants herbaceous, mostly biennial, sometimes winter annuals, or rarely short-lived perennials. Taproots long, vertical, thick, and usually woody above. Stems always arising from the center of a basal rosette, mostly solid, rarely hollow and inflated *(T. milleflorum)*, terete, slender to stout, sometimes very weak deriving support from being tangled among desert shrubs; usually glabrous and somewhat glaucous, or sparsely to densely hirsute to hirsute-hispid or pilose near the base, mostly glabrous above; simple or branched from the base, with the branches ascending or rarely subdecumbent, sometimes virgately branched above the base, often paniculately branched above; erect, straight, or rarely flexuous, 0.6–28 dm. high; caudex, when present, simple or branched, often covered with petiole bases of previous years. Trichomes simple, horizontal or retrorse, usually straight. Basal leaves somewhat thickish, rarely fleshy, always petiolate, not auriculate, glabrous to sparsely pubescent along the main veins or throughout, slightly to moderately glaucous, usually shed before fruit maturation, rarely persistent; apex acute to obtuse; cuneate to attenuate, rarely truncate, subcordate or obtuse at the base; oblanceolate to spatulate, less often oblong or lanceolate, sometimes ovate to obovate, rarely deltoid or elliptic in outline; margin entire to pinnately lobed, sometimes sinuate, lyrate, dentate, or repand, rarely laciniate or denticulate; 1.3–54 cm. long, 0.4–14.5 cm. wide; lobes, when present, 2–15, obtuse to acute, dentate or entire, less often sinuate to repand, rarely laciniate, sometimes decurrent on rachis, smaller and remote on lower portion of the leaf, divisions between lobes extending to midrib below, becoming gradually shallower towards the leaf apex, oblong to ovate, sometimes linear; petioles slender to stout, glabrous or ciliate, sometimes sparsely to densely pubescent, more or less expanded at the base,

0.5–15 cm. long. Cauline leaves petiolate or sessile, similar in shape and margin to basal leaves when petiolate, but gradually reduced in size upwards, with the uppermost leaves linear to lanceolate, acuminate to acute, entire or variously toothed or lobed; when sessile, cauline leaves ascending or partly to completely appressed to stem, acute to acuminate or rarely obtuse at apex, entire or rarely denticulate to repand, amplexicaul to sagittate and auriculate at base, or basal lobes absent (*T. integrifolium*), somewhat glaucous, glabrous to sparsely pubescent along the midrib and margin, linear to linear-lanceolate or lanceolate, sometimes oblong, rarely ovate, 0.7–19.5 cm. long, 0.2–3 cm. wide; basal lobes obtuse to acute, rarely acuminate, entire, ovate or oblong to linear or lanceolate, 0.1–2.3 cm. long, 0.5–11 mm. wide. Inflorescence mostly branched, densely flowered to lax, ebracteate, racemose or corymbose, slightly to greatly elongated in fruit, up to 10.2 dm. long. Floral buds oblong, linear, ovate, lanceolate, or sometimes clavate or subobpyriform, terete or less often quadrangular. Flower pedicels slender or sometimes stout, often slightly to strongly flattened at the base, ascending to divaricately ascending, divaricate, or rarely horizontal, straight, lowermost pedicels sometimes from the axils of uppermost cauline leaves. Calyx tubular, campanulate, nearly rotate, rarely urceolate. Sepals glabrous, greenish above and white below or vice versa, white, lavender, or purplish throughout, with or without a subapical callus, equal or unequal at base, saccate or nonsaccate, margin entire and more or less scarious, obtuse or rarely acute to acuminate at apex, rarely hooded, straight to slightly incurved, rarely coiled, erect or slightly to widely spreading, sometimes variously reflexed at anthesis, oblong, oblong-lanceolate, linear, or ovate, 2.5–11.5 mm. long, 0.75–3 mm. wide; lateral (usually inner) sepals often wider, more saccate, and inserted below the median (usually outer) sepals. Petals differentiated into claw and blade or not, crisped between claw and blade or along the blade, or not crisped, white, lavender, or purple, obtuse, subtruncate, rarely acute or retuse at apex, entire to slightly repand, veins often conspicuous and sometimes darker in color than the rest of the blade, spreading or with erect claws and horizontal to slightly reflexed blades, 2.5–22 mm. long; blades linear, oblanceolate, spatulate, narrowly to broadly obovate, 0.3–6 mm. wide; claws erect to slightly spreading, terete or flattened, sometimes deltoid-lanceolate with truncate base, glabrous or rarely covered with short gland-like trichomes near the base, 1–11 mm. long, 0.5–2 mm. wide. Stamens equal in length or tetradynamous; filaments terete, straight in the bud, filiform, slender to somewhat thickened, slightly dilated at the base, glabrous or rarely covered with gland-like trichomes near the base, straight to somewhat recurved, erect to spreading at anthesis, white or lavender to purple; filaments of single (lateral) stamens inserted on same level or lower than paired (median) filaments, straight or strongly curved at the base, 2–14.5 mm. long; paired filaments straight at base, free or very seldom partially to completely fused, 3–15.5 mm. long; anthers lavender to purple, apiculate or not, sagittate at the base, introrse, basifixed, exserted or partially to completely included, recurved to circinately coiled when fully dehisced, linear, oblong, or ovate, 1–6 mm. long. Glandular tissue usually low, disc-like; median glands subtending base of paired filaments, or absent; lateral glands present, surrounding base of single filaments, usually emarginate on the inner side, or sometimes open, usually extending laterally between petal insertion and pistil, flat or 2-toothed on the inner side. Fruiting pedicels slender to stout, slightly to strongly flattened at the base, or not flattened, often faintly striate, straight or incurved, usually expanded at the tip, glabrous, erect, ascending, divaricately ascending, divaricate, horizontal, or variously reflexed, usually persistent, 0.1–3.5 cm. long. Siliques dehiscent, narrowly linear, stipitate, mostly torulose, rarely submoniliform or plain (smooth valved), terete or somewhat flattened parallel to the septum, or rarely quadrangular, straight or slightly to strongly incurved, rarely flexuous, erect and sometimes appressed to the rachis, ascending, divaricately ascending, variously spreading, or reflexed, 0.6–12.1 cm. long, 0.5–2.3 mm. wide; valves 2, glabrous, usually convex, with a prominant midvein extending full length, secondary veins often less conspicuous, sometimes forming a reticulum; replum mostly straight, rarely constricted between seeds; septum translucent to brown, with or without a differentiated central band of longitudinally arranged elongated cells. Styles slender to

stout, cylindrical, subconical, or subclavate, 0.2–5 mm. long. Stigmas small, entire or very rarely slightly 2-lobed, usually smaller in diameter than style. Gynophores slender to stout, 0.2–8.5 mm. long. Seeds brown to yellow-brown, uniseriate, oblong to ovate, faintly reticulate, non-mucilaginous, few to numerous per locule, wingless or rarely with a minute appendage at the distal end, terete to flattened, 0.75–2.3 mm. long, 0.5–1.25 mm. wide; cotyledons mostly oblique, rarely accumbent or incumbent, retuse or obtuse at apex.

Flowering January to October at elevations from 100 to 10,500 feet in western United States, northern Mexico, and southwestern Canada.

KEY TO THE SPECIES OF THELYPODIUM

A. Cauline leaves petiolate, at least the lower and middle ones pinnately to lyrately lobed, sometimes dentate; siliques flattened parallel to the septum or terete; styles subclavate to subconical; sepals, petals, and stamens spreading to erect near the base at anthesis.

B. Filaments and claws covered with short gland-like trichomes on their lower half; siliques smooth, neither torulose nor submoniliform; upper parts of the stem and rachis often sparsely pubescent; northern Mexico. ..... 18. *T. paysonii.*

B. Filaments and claws glabrous throughout; siliques torulose or sometimes submoniliform; upper parts of stem and rachis almost always glabrous.

C. Inflorescence a densely flowered elongated raceme, (0.3)0.8–8.1(10.2) dm. long; sepals, petals, and filaments erect at the base; petals differentiated into claw and blade, (6)8.5–18(20) mm. long; claws deltoid to deltoid-lanceolate, thickish, flattened and broadest at the base, (2.5)3–6(7) mm. long; filaments (4.5)6.5–14(15.5) mm. long; fruiting pedicels stout.

D. Fruiting pedicels straight, horizontal; stems solid, not inflated; basal and lower cauline leaves pinnately lobed to laciniate; petioles of basal leaves glabrous; siliques spreading; petal blades linear, 0.3–0.7(1.5) mm. wide; widely distributed ..... 1. *T. laciniatum.*

D. Fruiting pedicels strongly curved upwards, with the tips usually erect; stems almost always hollow at least to the inflorescence, often slightly to moderately inflated below; basal and lower cauline leaves often dentate to sinuate, rarely laciniate or pinnately lobed; petioles of basal leaves ciliate at least near the base; siliques erect to divaricately ascending, often partly or completely appressed to the rachis; petal blades oblanceolate to spatulate, 1–2 mm. wide; widely distributed ..... 2. *T. milleflorum.*

C. Inflorescence dense to lax, corymbose to short racemose, 0.15–0.5 (0.7) dm. long; sepals spreading; petals spreading to erect, usually not differentiated into claw and blade, or if so, then claws cylindrical, slender, and uniform in width, claws 1–2.5(3) mm. long; filaments erect to spreading, 2.5–6.5(8.5) mm. long; fruiting pedicels slender.

E. Sepals ascending, sometimes spreading or erect; filaments and petal bases erect; siliques submoniliform, terete, replum mostly constricted between the seeds; stems pubescent near the base to glabrous; Utah, Nevada, and western Colorado ..... 14. *T. laxiflorum.*

E. Sepals widely spreading; filaments and petals spreading; siliques torulose, mostly flattened parallel to the septum, replum straight; stems glabrous.

F. Fruiting pedicels filiform or at most very slender, divaricately ascending, 2–3.5 cm. long, southwestern Texas ..... 17. *T. tenue.*

F. Fruiting pedicels rigid, slender to somewhat stoutish, widely divaricate to variously reflexed, 0.4–1.4(1.7) cm. long.

G. Flowers lavender to purple; petals (2.5)3–4.5 mm. long, 0.5–1 mm. wide; filaments 2.5–3.75 mm. long; basal and lower cauline leaves greyish, fleshy, ovate or less often obovate to elliptic, repand or sometimes sinuate or lyrate; central Idaho ..... 15. *T. repandum.*

G. Flowers mostly white, rarely lavender throughout; petals (3.5)4–7.5 (9) mm. long, 1–2 mm. wide; filaments (3)4–6.5(8.5) mm. long; basal and lower cauline leaves usually green, thin to somewhat thickish, lanceolate or oblanceolate, mostly pinnately lobed, rarely lyrate.

H. Plants biennial; styles clavate to subclavate; uppermost cauline leaves entire or rarely lobed; stems (1.5)3.2–16.3(28) dm. high; petals oblong to linear, differentiated into claw and blade; Arizona, southeastern Colorado, northern Mexico, New Mexico, northwestern Oklahoma, and southwestern Texas ..... 13. *T. wrightii.*

H. Plants annual; styles conical to subconical; uppermost cauline leaves mostly pinnately lobed; stems 1.3–4.8(6.1) dm. high; petals spatulate to oblanceolate, attenuate to short claw-like base; southwestern Texas .. 16. *T. texanum.*

A. Cauline leaves sessile, sagittate, amplexicaul, or auriculate at the base, lower and middle leaves mostly entire, rarely dentate; siliques terete, styles cylindrical or more often tapering toward apex; at anthesis, sepals, petals, and filaments usually erect near their bases.

I. Plants perennial; caudex woody, thick, covered with papery remains of petiole bases of previous growth seasons; stems rather weak, usually flexuous, few leaved (usually 4 or less); basal leaves persistent throughout the growth season; petioles glabrous at the base; northeastern California, Oregon, Nevada, and western Idaho ..... 12. *T. flexuosum.*

I. Plants biennial, or if perennial, then rootstock slender, nearly naked; stems erect, slender or stout, few to several leaved; basal leaves usually withering early in the growth season, or if somewhat persistent, then petioles ciliate near the base.

J. Cauline leaves attenuate at base, ascending, not appressed to stem, neither sagittate nor amplexicaul, auricles absent; median glandular tissue absent; widely distributed ..... 7. *T. integrifolium.*

J. Cauline leaves sagittate, amplexicaul, or sometimes auriculate at the base, appressed or ascending, auricles well-developed to reduced; median glandular tissue present or absent.

K. Terminal branch of the inflorescence racemose, elongated to somewhat shortened, lax to congested.

L. Inflorescence a densely flowered spike-like raceme; flowers mostly white, rarely lavender with a laxer inflorescence, fruiting pedicels erect or less than 2.5 mm. long; petal blades crisped throughout.

M. Fruiting pedicels erect to erect-ascending, partly or completely appressed to rachis, slender, not flattened at the base, (1.5)2–5 (10) mm. long; floral buds and sepals usually oblong to linear-oblong, seeds ± flattened, 1–1.5(1.75) mm. long, 0.5–0.75(1) mm. wide; Nevada and eastern California ..... 3. *T. crispum.*

M. Fruiting pedicels horizontal or sometimes divaricate, rather stout, flattened at the base, 1–2(2.5) mm. long; floral buds and sepals ovate to lanceolate-ovate, acuminate; seeds plump, (1.3)1.5–2 mm. long, (0.75)1(1.25) mm. wide; Oregon and northern California ..... 4. *T. brachycarpum.*

L. Inflorescence mostly a lax raceme; flowers lavender to purple, rarely white, fruiting pedicels widely spreading or ascending; petal blades not crisped or only crisped at their junction with the claws.

N. Filaments of paired stamens partly to completely fused; Oregon and northern California ..... 9. *T. howellii.*

N. Filaments of paired stamens completely free.

O. Petals narrowly linear, 0.3–0.5(0.75) mm. wide; floral buds linear to narrowly oblong; southern California ..... 8. *T. stenopetalum.*

O. Petals narrowly spatulate to somewhat oblanceolate, (0.5)1–3(4) mm. wide; floral buds mostly ovate to lanceolate, if linear or narrowly oblong, then inflorescence slightly congested and petals dark purple.

P. Floral buds narrowly oblong to linear; gynophore (1)2.5–6(7.5) mm. long; perennial; anthers completely exserted; central Oregon. ..... 5. *T. eucosmum.*

P. Floral buds ovate to lanceolate; gynophore (0.2)0.5–1(3.5) mm. long; almost always biennials; anthers often partly to completely included.
Q. Fruiting pedicels ascending, mostly straight, not flattened at the base; siliques ascending, straight, pedicels and siliques usually in a straight line; basal leaves oblong to oblong-lanceolate; eastern Oregon . 9. *T. howellii.*
Q. Fruiting pedicels divaricate, divaricately ascending, horizontal, mostly curved upwards, often slightly flattened at the base; siliques straight to curved, usually with erect tips, siliques and pedicels usually forming an arc; basal leaves mostly ovate to oblanceolate; widely distributed, but absent from Oregon ..... 10. *T. sagittatum.*
K. Terminal inflorescence distinctly corymbose.
R. Cauline leaves partly or completely appressed to stem, linear to linear-lanceolate; basal leaves mostly dentate or repand, 1.3–4(7) cm. long, (0.4) 0.6–1.8 cm. wide, petioles glabrous; anthers exserted, calyx usually 4-sided; inflorescence slightly elongated in fruit; siliques slender, strongly incurved, young siliques extending above the top of inflorescence; stems (4)6–16(20) dm. high; floral buds oblong; central Utah ..... 6. *T. rollinsii.*
R. Cauline leaves ascending, oblong to lanceolate; basal leaves entire, (2)6–20(29) cm. long, (0.6)1–4(5) cm. wide, petioles ciliate near the base; anthers partly to completely included; calyx usually cylindrical, or slightly flattened; inflorescence greatly elongated in fruit; siliques usually stout, straight to somewhat curved, young siliques not extending above the top of inflorescence; stems (1.4)2–8(12) dm. high; floral buds ovate.
T. Siliques (0.5)0.75–1.(1.2) mm. wide; petals (0.5)1–3(4) mm. wide; median glandular tissue mostly absent; seeds somewhat flattened, (0.75)1–1.3(1.5) mm. long; widely distributed ..... 10. *T. sagittatum.*
T. Siliques (1.3)1.5–2.3 mm. wide; petals 2.5–5(6) mm. wide; median glandular tissue mostly present; seeds plump (1.3)1.5–2 mm. long; western Wyoming, northeastern Idaho, and adjacent Montana ... 11. *T. paniculatum.*

1. **Thelypodium laciniatum** (Hooker) Endlicher

Macropodium laciniatum Hook., Bot. Miscell. 1:341. 1830. Type: dry rocks about Wallawallah, and at Priest's Rapid on the Columbia, *Douglas s.n.* (K), not seen.

Pachypodium laciniatum (Hook.) Nutt. in Torr. & Gray, Fl. N. Am. 1:96. 1838.

Thelypodium laciniatum (Hook.) Endl. in Walp. Repert. 1:172. 1842.

Thelypodium streptanthoides Leib., Contr. U. S. Nat. Herb. 11:299. 1906. Holotype: near Wilson Creek, alt. 680 m., Douglas Co., Washington, June 19, 1893, *J. H. Sandberg & J. B. Leiberg 229* (US); isotype: US.

Thelypodium laciniatum (Hook.) Endl. var. *streptanthoides* (Leib.) Pays., Ann. Mo. Bot. Gard. 9:274. 1923.

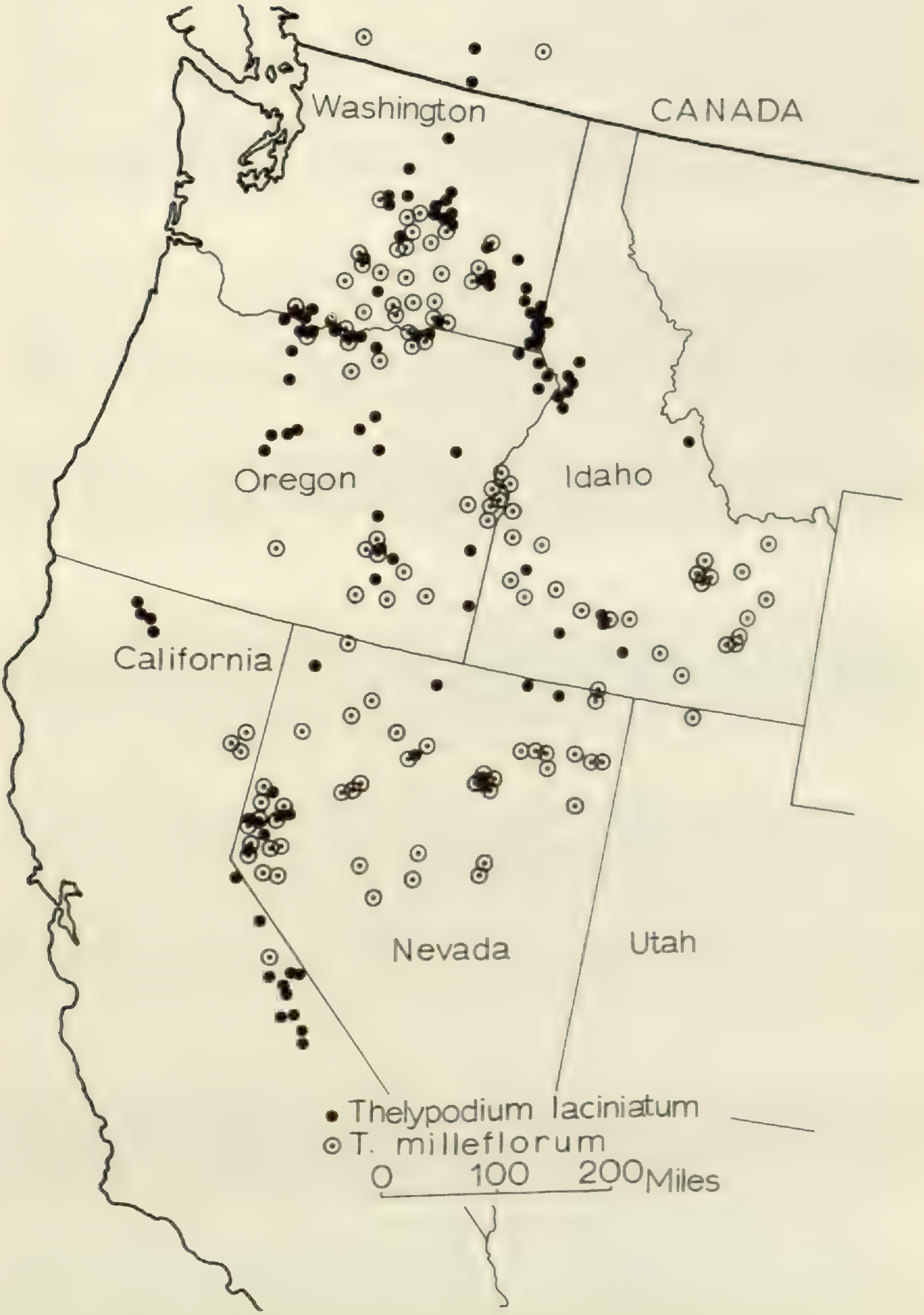
Thelypodium leptosepalum Rydb., Bull. Torr. Bot. Club 34:433. 1907. Holotype: Lewiston, Nez Perce Co., Idaho, May 6, 1896, *A. A. & E. G. Heller 3022* (NY); isotypes: MO,ND-G,UC,US.

Plants biennial; stems erect, often virgately branched above the base, sometimes simple or branched from the base, glabrous and somewhat glaucous, solid, (1.3)2.6–10.0(14.5) dm. high; basal leaves and lower cauline leaves petiolate, glabrous and somewhat glaucous, usually thickish, (4.3)6.8–24(45) cm. long, (1)1.8–8.5(14) cm. wide, lanceolate to deltoid-lanceolate, less often oblong to ovate, rarely deltoid, acute, mostly truncate to cuneate at base, lanciniate to pinnately lobed; lobes usually oblong to ovate, smaller and remote on lower part of the leaf, acute to rarely obtuse, sinuate to dentate, rarely laciniate to repand or entire, divisions between lobes usually extending to midrib below and becoming gradually shallower toward leaf apex; petioles somewhat expanded at base, glabrous, (1)1.5–10(15) cm. long; cauline leaves reduced upwards, lanceolate to linear-lanceolate, often acuminate, entire to sinuately toothed or laciniate; inflorescence a densely flowered raceme, rarely lax, slightly elongated in fruit, usually branched, (0.3)0.8–6.2(9.5) dm. long; calyx somewhat urceolate to rarely tubular; sepals creamy white above

and green below or lavender to purple throughout, glabrous, oblong to linear-oblong, rarely oblong-lanceolate, obtuse, scarious at margin, becoming somewhat papery when dry, equal and uniformly saccate at the base, rarely non-saccate, erect, (3.5)4–7.5(9.5) mm. long, (0.75)1–2(2.5) mm. wide; petals white to purple, (6)8.5–18(20) mm. long, 0.3–0.75 (1.5) mm. wide, differentiated into claw and blade, with the blade papery, slightly crisped, linear or sometimes narrowly linear-lanceolate, obtuse to acute; claws erect, thickish, narrowly deltoid-lanceolate, truncate and distinctly expanded at the base, (2.5)3–6(7) mm. long, 1–2 mm. wide; filaments white to purple, nearly equal in length, (4.5)6.5–12(15) mm. long, usually erect below and spreading above, filaments of single stamens strongly curved at the base; anthers well exserted above the calyx, linear, rarely oblong, usually purple, apiculate, sagittate at base, circinately coiled when fully dehisced, 2–4(5.5) mm. long; glandular tissue continuous and disc-like, slightly raised above the receptacle, subtending base of paired filaments, often completely surrounding base of single filaments, well-developed opposite petal insertions, occasionally extending between the insertion areas of the paired filaments and the gynophore; fruiting pedicels horizontal to rarely divaricate, straight or sometimes slightly curved, usually stout, often flattened at the base, (2)3–6.5(15) mm. long; siliques somewhat flattened parallel to septum to terete, rarely 4-sided, torulose, straight to curved, sometimes irregularly flexuous, widely spreading to divaricately ascending, rarely recurved, (2.5)3.4–10(12.1) cm. long, (0.75)1–1.5(2) mm. wide; gynophores slender to stout, (0.5)1–5(8.5) mm. long; styles stout, cylindrical to occasionally subclavate, (0.3)0.75–2.5(4) mm. long; stigmas entire; seeds (0.75)1–1.5(1.75) mm. long, 0.5–0.75(1) mm. wide; cotyledons oblique, very rarely accumbent.

Flowering from middle April to early August, but mainly from early May through June at elevations from 100 to 8,000 feet above sea level. Distributed in northern and western Nevada, northern and eastern California, Oregon and western Idaho, northward through southern and central Washington to southern British Columbia (Map 1).

REPRESENTATIVE SPECIMENS. **Canada: British Columbia.** Lake Osoyoos, between lat. 40° and lat. 49°05′, long. 119°20′ and long. 119°35′, *Macoun 70851* (F,GH,NY). **California. Alpine Co.:** 4.2 miles E. of Woodfords, *Breedlove 3587* (GH); Bishop Creek, *Alexander & Kellogg 4250* (DS,UC,US,UTC); **Inyo Co.:** S. of Fish Springs in Owens Valley, *DeDecker 1754* (GH); W. of Big Pine, *Heller 8262* (CAS,DS,F,GH,MO, NY,PH,UC,US); **Mono Co.:** 6 miles N.E. of Bridgeport on California Hwy. 182, *I. & M. Al-Shehbaz 68112* (GH); 18.5 miles N. of Bishop on U.S. Hwy. 395, *I. & M. Al-Shehbaz 68119* (GH); 21 miles S.E. of Lee Vining, *Rollins 57349* (F,GH,MICH, MO,NY,UC); Benton, *Tidestrom 9990* (F,GH,NY,US); **Siskiyou Co.:** 2.8 miles N. of jct. U.S. Hwy. 97 and California Road A-12, *I. & M. Al-Shehbaz 68134* (GH); Laird's Landing, *Peirson 3734* (CAS,RSA). **Idaho. Ada Co.:** Swan Falls power plant, *Maguire & Holmgren 26192* (NY,UTC); **Gooding Co.:** 2.8 miles S. of jct. U.S. Hwys. 30, 26 & 20 on Hwy. 30, *I. & M. Al-Shehbaz 68152*(GH); **Idaho Co.:** Rocky Canyon Creek near Cottonwood, *Christ 10038* (NY); 5 miles S. of Whitebird, *Hitchcock & Muhlick 8482* (DS,NY,UTC,WS,WTU); Snake River Canyon near mouth of Sheep Creek, *Meyer 263* (MO,RSA,WS); ½ mile up Divide Creek from Snake River, *Packard 410* (GH,MO,UC, US,WS); **Lemhi Co.:** ca. 2 miles E. of Indianola Ranger Station, north bank of Salmon River, *Hitchcock & Muhlick 14320* (DS,MO,NY,RSA,UC,UTC,WS,WTU); **Nez Perce Co.:** Lewiston Hill, *Hitchcock & Samuel 2952* (CAS,DS,LA,OSC,POM,RM); Valley of Peter Creek, *Sandberg, MacDougal & Heller 122* (CAS,DS,F,GH,NY,ORE,POM,US); **Owyhee Co.:** Indian Hot Springs Falls, ca. 12 miles S.E. of Bruneau, *Hitchcock & Muhlick 23649* (WTU); **Twin Falls Co.:** Shoshone Falls, *I. & M. Al-Shehbaz 68153* (GH); Twin Falls and Shoshone Falls, *Nelson & Macbride 1343* (DS,F,GH,MO,NY,POM, RM,UC,US,UTC,WS,WTU). **Nevada. Elko Co.:** Victory Hwy., Humboldt Cañon, *Eastwood & Howell 238* (CAS,GH); Owyhee, *Jones 25314* (CAS,DS,MO,ND–G,POM); **Eureka Co.:** Palisade, *Jones 3767* (CAS,DS,MO,NY,POM,RM,UC,US,UTC); **Humboldt Co.:** S. & E. of Hinkey Summit of Santa Rosa Range of Humboldt National Forest, *Constance, Molseed*



MAP 1. Distribution of *Thelypodium laciniatum* and *T. milleflorum*.

& *Ornduff 3728* (NY,TEX,UC,UTC); **Ormsby Co.:** Carson City, *Jones s.n.*, 1897 (CAS, MO,POM,RM,US,UTC); **Storey Co.:** 3¼ miles N. NW. of 5-mile House, *Adams 158* (RSA,UC); **Washoe Co.:** Pyramid Lake, *Kennedy 1003* (NY,RM,US); Badger Mountain, Sheldon Antelope Range, *Murie 2868* (NA). **Oregon. Baker Co.:** 22 miles N.E. of U.S. Hwy. 26 and Oregon Hwy. 7 intersection, *Davidse & Collotzi 514* (NY,UTC,WTU); **Crook Co.:** along Rimrock above Crooked River Valley, ½ mile W. of Prineville, *Kruckeberg 2171* (COLO,NY,RM,RSA,UC,WS,WTU); **Deschutes Co.:** 5 miles below Bend, near Deschutes River, *Peck 9718* (GH,MO,NY,WTU); **Douglas Co.:** 3 miles S. of Yoncalla, *Gale 187* (DS); **Gilliam Co.:** 5 miles W. of Blalock on U.S. Hwy. 30 along Columbia River, *I. & M. Al-Shehbaz 68145* (GH); Pine Creek, *Leiberg 172* (GH,MO, NY,ORE,POM,US); **Grant Co.:** walls of John Day Canyon, *Henderson 5295* (CAS,DS, GH,MO,ORE); 7 miles from Vantage Bridge on road to Quincy, *Howell 28470* (CAS,GH, WTU); S. of Narrows, *Ripley & Barneby 6096* (GH); **Hood River Co.:** near Hood River, *Leach s. n.*, 1927 (WTU); base of Rowena Loops, Columbia Gorge, *Thompson 4318* (DS,MO,WTU); **Malheur Co.:** about 20 miles W. of Jordan Valley, Twp. 30 S., R. 44 E., S. 19, *Cronquist 8389* (CAS,MICH,NY,RM,RSA,TEX,UC,UTC,WS,WTU); **Morrow Co.:** Ione, *Lunell s.n.*, 1903 (RM); **Sherman Co.:** W. side of John Day River, *Hitchcock 20442* (COLO,NY,WS,WTU); **Umatilla Co.:** 15 miles E. of Umatilla, *Maguire 15169* (UTC); **Wallowa Co.:** near mouth of Deep Creek, T. 4 N., R. 49 E., *Constance, Rollins & Dillon 1574* (DS,GH,MO,ND,US,WS,WTU); between Cow Creek Bridge and mouth of Imnaha River, *Kruckeberg 2317* (COLO,NY,RM,RSA,UC,WS,WTU); **Wasco Co.:** Indian Head Canyon in Warm Springs Indian Reservation, *French 182* (UC); The Dalles, *Howell s.n.*, 1880 & 1881 (CAS,F,MICH,NA,NY,ORE,PH,US); **Wheeler Co.:** 6.2 miles W. of jct. U.S. Hwy. 26 and Oregon Hwy. 19, *I. & M. Al-Shehbaz 6955* (GH). **Washington. Adams Co.:** 2 miles N. of Macall, *Jeffrey s.n.*, 1946 (NY,UC,WS); **Asotin Co.:** S.W. of Anatone, Twp. 7 N., R. 44 E., S. 35, *Cronquist 5710* (GH,NY,RSA,UC,US, UTC,WS,WTU); 5 miles below mouth of Grande Ronde River, *M. & R. Owenby 2059* (CAS,COLO,DS,GH,MO,NA,NY,ORE,OSC,PH,RSA,TEX,UC,US,UTC,WIS,WS,WTU); **Chelan Co.:** 6 miles N. of Wenatchee, *Hitchcock 17363* (COLO,DS,GH,NY,RM,RSA,UC,US,UTC,WS,WTU); **Douglas Co.:** between Coulee City and Waterville, *Spillman s.n.*, 1896 (WS); **Franklin Co.:** Palouse Falls, *Daubenmire 37236* (WS,WTU); **Garfield Co.:** Wawawai Ferry, *St. John 6076* (UC,WS); **Grant Co.:** 8 miles N. of Dry Falls, *Rogers 599* (CAS, DS,GH,MO,NY,POM,UC,US,UTC,WIS,WS,WTU); near Soap Lake, *Thompson 11492* (CAS,DS, GH,MO,NY,PH,POM,WTU); **Kittitas Co.:** near Ellensberg, *Jones 10161* (WIS); **Klickitat Co.:** Lyle, *Suksdorf 841* (DS,F,MO,NY,UC,US,WS); **Okanogan Co.:** W. of Hess Lake, *Fiker 895* (DS,US,WS); **Walla Walla Co.:** Wallula, *Booth s.n.*, 1942 (WS); **Whitman Co.:** N. bank of Snake River opposite Clarkston, *Constance, Clarke, Dillon, Machlis & Rollins 1056* (DS,F,GH,MO,NY,OSC,PH,RM,UC,US,UTC,WIS,WS,WTU); Almota, *Constance, Clarke, Machlis & Rollins 1077* (CAS,F,GH,JEPS,MO,NY,OSC,PH,RM,UC,UTC,WIS,WS,WTU); **Yakima Co.:** mouth of Selah Creek, E. of U.S. Hwy. 97, *Witt 1929* (NY,WS,WTU).

Thelypodium streptanthoides of Leiberg is very similar to *T. laciniatum* in every character but flower color. The other characters that are said to separate the two (thin and non-glaucous leaves in the former versus thick and glaucous leaves in the latter) often break down within the same population. Such characters were questioned by Payson (1923) who suggested that *T. streptanthoides* may only deserve the rank of a form. The calyx is said to be saccate in *T. streptanthoides* and not so in *T. laciniatum* (Hitchcock, 1964). However, this character is also found to be inconsistent within each of the two color forms. The purple-flowered form (*streptanthoides*)is restricted to the northern portion of the species range, while the white-flowered form is distributed throughout the range but less often in the north. The two forms seem to intergrade in a number of localities in northern Oregon and western Idaho. Intermediates with

various color intensities have been found. It is deemed wise, therefore, not to give any taxonomic recognition to the purple-flowered form.

Thelypodium laciniatum appears to grow primarily on silty (rarely sandy) soil in crevices of basalt cliffs or outcrops along roadsides and canyon walls. Occasionally it grows in association with sagebrush on gravelly or rocky hillsides. In addition to the common occurrence of this species on basaltic rocks, there are scattered collections made from "limestone ledges" (*St. John 3477*), "crevices of sandstone rocks" (*Rollins 57349*), "on serpentine rock and talus" (*Hitchcock & Muhlick 8482*), and "sandy bank" (*Hitchcock & Muhlick 14320*).

Thelypodium laciniatum shows great variation in basal leaf morphology. Such variation can usually be seen within any sizeable population. Plate 4 shows the variation in basal leaves of two population samples grown under uniform greenhouse conditions. The siliques show a considerable amount of variation in length. Silique width is much less variable. Plants of northern California tend to have broader siliques than those in other parts of the species range, but such a tendency does not provide the basis for division of the species into subspecific taxa.

Thelypodium laciniatum is most closely related to *T. milleflorum* which it resembles in many important morphological features. The latter has been considered to be a variety of *T. laciniatum* since Payson's treatment of the genus in 1923. The evidence presented by Payson to support such a placement is misleading. He claimed that the two species intergrade, and suggested that, since they have similar geographic distributions (Map 1), they are best treated as varieties of the same species. In fact, the two species are very distinct ecologically, and rarely grow in the same habitat. *Thelypodium laciniatum* tends to grow mostly on silty soils in crevices of basaltic cliffs or rocky outcrops, while *T. milleflorum* almost always grows on sandy soil in open desert or along river banks. The writer has collected the two species growing a few feet apart in one locality (near Beverly, Washington) where *T. milleflorum* was growing on sand accumulated at the base of a cliff along the Columbia River, and *T. laciniatum* was very abundant in the crevices of the same cliff. No hybrids were detected. Moreover, the two species found in this locality are chemically very distinct as they are elsewhere in their ranges (see the section on biochemical systematics). Of the two species, *T. milleflorum* appears to be more advanced morphologically than *T. laciniatum* from which it may have been derived.

The overall resemblances of *Thelypodium laciniatum* to certain species of the closely related genus *Stanleya* have been clearly pointed out by Rollins (1939). Several morphological features of the leaves, inflorescences, petals, stamens, nectar glands, and siliques are strikingly similar in these taxa. On the basis of such similarities, Payson (1923, p. 244) had suggested that *Thelypodium* may have been derived from *Stanleya*.

Thelypodium laciniatum is easily distinguished from *T. milleflorum* by its solid stems, basal and lower cauline leaves pinnately lobed to laciniate, glabrous petioles, fruiting pedicels straight and horizontal, siliques spreading to divaricate, and linear petal blades. In typical *T. milleflorum* the stems are almost always hollow, often slightly to moderately inflated below, the basal leaves and lower cauline leaves are often coarsely toothed to sinuate and rarely laciniate or pinnately lobed. The petioles of the basal leaves, and occasionally the lower cauline leaves, are ciliate at least near the base. Fruiting pedicels are strongly curved upwards and the siliques are erect to divaricately ascending, often partly or completely appressed to the rachis. Finally, the petal blades are mostly oblanceolate and rarely spatulate or narrowly oblanceolate.

Most of the above morphological differences have been, unfortunately, overlooked. The morphological, ecological, and chemical differences are clearly sufficient to maintain the two taxa as distinct species. This interpretation is further strengthened by the fact that no hybrids were detected in an area where the two species were growing together.

2. **Thelypodium milleflorum** Nelson

Thelypodium milleflorum Nels. Bot. Gaz. 52:263. 1911. Holotype: New Plymouth, Payette Co., Idaho, June 10, 1910, *J. F. Macbride* 234 (RM); isotypes: DS,F,GH,MO, NY,UC,US,WS.

Thelypodium laciniatum (Hook.) Endl. var. *milleflorum* (Nels.) Pays., Ann. Mo. Bot. Gard. 9:274. 1923.

Plants biennial; stems erect, single from the base, often branched above, glabrous and glaucous, almost always hollow at least to the inflorescence, often slightly to moderately inflated above the base, usually purple below and creamy white above, (1.8)4.5–13(21) dm. high; basal and lower cauline leaves petiolate, glabrous and somewhat glaucous, usually thickish, mostly oblong to narrowly oblong, sometimes ovate or lanceolate, acute at apex, cuneate or rarely obtuse to subcordate at the base, margin often variously dentate to sometimes sinuate, rarely repand or laciniate to pinnately lobed, (3.8)6–23(28) cm. long, (0.9)2–6.5(10) cm. wide; petioles of basal leaves and sometimes lowermost cauline leaves ciliate, at least near the base, (1) 1.8–9.5(13) cm. long, petioles of upper cauline leaves glabrous and shorter; upper cauline leaves lanceolate, acute to acuminate, mostly entire; inflorescence a densely flowered raceme, slightly elongated in fruit, (0.5)1.7–8.1(10.2) dm. long, with the rachis often whitish; flowers numerous; flower pedicels whitish, slender, straight, horizontal to divaricate; sepals creamy white, equal and uniformly saccate at base, oblong to linear–oblong, obtuse, scarious at the margin, often becoming somewhat papery when dry, erect, (4)4.5–8(9) mm. long, 1–2 mm. wide; petals white, differentiated into claw and blade, (7)9–15(16) mm. long, blades 1–2 mm. wide, mostly oblanceolate, rarely spatulate to narrowly oblanceolate, obtuse to nearly truncate, somewhat papery; claws thickish, erect, narrowly deltoid-lanceolate, truncate and distinctly expanded at the base, (3)3.5–5.5(6) mm. long, 1–2 mm. wide at the base; filaments white, slender, erect below, somewhat ascending above, nearly equal in length, (6)7–14.5(15.5) mm. long; anthers linear to narrowly oblong, apiculate, sagittate at base, circinately coiled when fully dehisced, well exserted above the calyx, often purple, 2.5–4.5(6) mm. long; glandular tissue continuous, slightly raised above the receptacle, subtending base of paired stamens, surrounding base of single stamens, more developed opposite petal insertions; fruiting pedicels slightly flattened at base, strongly curved upwards, with the tips erect, usually stout, (1.5)2.5–5(7) mm. long; siliques somewhat flattened parallel to septum, rarely terete, narrowly linear,

torulose, erect to ascending or sometimes divaricately ascending, often partly or completely appressed to rachis, straight to somewhat irregularly flexuous, (1.8)3.3–8.5(10) cm. long, (0.75)1–1.5(1.75) mm. wide; gynophores stoutish, (0.5)1–4(6) mm. long; styles stout, cylindrical to nearly subclavate, (0.5)0.75–1.5(3) mm. long; stigmas entire; seeds (0.75)1–1.5(2) mm. long, 0.5–0.75(1) mm. wide; cotyledons oblique, very rarely accumbent.

Flowering from middle April through early August but mainly early May to early July at elevations from 500 to 7,100 feet in western and southern Idaho, northwestern Utah, northern and central Nevada, northeastern California, Oregon, southern and central Washington (Map 1).

REPRESENTATIVE SPECIMENS. **Canada. British Columbia:** Hope, *Anderson 732* (WS); Penticton, *Anderson 733*(WS). **California. Lassen Co.:** 2 miles N. of Mapes on N. side of Honey Lake Valley, *Babcock & Stebbins 1782* (RM,UC); **Mono Co.:** along Deep Wells road S.E. of Mono Lake, Sec. 3 & 4, T. 2 N., R. 26 E., *J. & A. Reveal 412* (UTC). **Idaho. Ada Co.:** along hwy. E. of Boise, *Cronquist 142–36* (UTC); **Bannock Co.:** Pocatello, *Blankinship s.n.*, 1902 (GH,RM); **Bingham Co.:** Blackfoot, *Jones s.n.*, 1909 (POM); **Bonneville Co.:** Idaho Falls, *E. & L. Payson 1728* (CAS,GH,MO,NY,RM, UC); **Butte Co.:** 2 miles N. of Butte City, *Hitchcock & Muhlick 22753* (DS,NY,OSC, TEX,UC,UT,WS,WTU); Arco, *Macbride & Payson 3094* (CAS,DS,GH,MO,NY,POM,RM,UC, US); **Canyon Co.:** Caldwell, *Tucker 609* (NY); **Cassia Co.:** Malta, *Cottam 3008* (UT); **Clark Co.:** 9 miles S.W. of Dubois, *Hitchcock & Muhlick 22785* (COLO,NY,WS,WTU); **Elmore Co.:** 14 miles N.W. of Glenns Ferry, *Rollins 1157* (MO,NY); **Gooding Co.:** 8 miles S. of Gooding, *Christ & Ward 7188* (NY); **Jefferson Co.:** ca. 12 miles N.E. of Howe, *Hitchcock & Muhlick 21290* (NY,WS,WTU); **Lincoln Co.:** 16.2 miles S.E. jct. of U.S. Hwy. 26 and Idaho Hwy. 23 below Carey, *I. & M. Al-Shehbaz 68154* (GH); **Minidoka Co.:** Heyburn, *Christ 9499* (NY); **Payette Co.:** 5 miles S.W. of Fruitland, *Christ 9433* (NY); **Owyhee Co.:** 2 miles S. of Murphy, *Hitchcock & Muhlick 22569* (NY,WTU); **Washington Co.:** Olds Ferry, *Christ 9378* (NY). **Nevada. Churchill Co.:** 1 mile W. of Eastgate, *Mills & Beach 664* (NA); **Elko Co.:** 10 miles S. of Montello on Nevada Hwy. 30, *I. & M. Al-Shehbaz 6898* (GH); 29 miles N.E. of Elko on Interstate Hwy. 80, *I. & M. Al-Shehbaz 68104* (GH); Sprucemont, *Jones s.n.*, 1891 (GH, NY,ORE,POM,RM,TEX,UC,US,WS,WTU); **Eureka Co.:** 14.3 miles N. of Eureka on Nevada Hwy. 51 from its jct. with U.S. Hwy. 50, *I. & M. Al-Shehbaz 68106* (GH); Palisade, *Jones 3772* (CAS,DS,NY,POM,UC,US,UTC); 5 miles W. of Eureka, *Rollins & Chambers 2540* (DS,GH,RM,UC,UTC); **Humboldt Co.:** 11 miles W. of Winnemucca on Nevada rd. 49, T. 36 N., R. 36 E., Sec. 28, *N. & P. Holmgren 3964* (GH); 13 miles N. of Sulphur on road to Quinn River Crossing, T. 35 N., R. 29 E., *N. & P. Holmgren 4032* (GH); **Lander Co.:** 3 miles N. of Nye and Lander Co. line, mouth of Kingston Canyon, *Train 2765* (DS,NA,NY); **Lyon Co.,** 10 miles N.E. of Dayton on U.S. Hwy. 50, *Weber & Rose 8404* (COLO,DS,RSA,TEX,UC,WTU); **Nye Co.:** near Ione, *Beach 62* (NA); **Ormsby Co.:** Eagle Valley, *Baker 1020* (F,GH,MO,NY,POM,RM,UC,US); **Pershing Co.:** 4.5 miles N. of Lovelock, *Alexander & Kellogg 4606* (DS,UC,UTC); **Washoe Co.:** 3.9 miles S.S.W. of Pyramid, *Simontacchi 508* (NA,UC). **Oregon. Gilliam Co.:** 5 miles W. of Blalock, *Raven 18388* (GH); **Harney Co.:** 26 miles S. of Folly Farm in T. 32 S., R. 35 E., *Hitchcock & Muhlick 21129* (DS,NY,RM,WS,WTU); **Lake Co.:** 20 miles N. of Paisley, *Leach s.n.*, 1927 (ORE); **Malheur Co.:** 11 miles S.E. of Vale in T. 19 S., R. 43 E., S. 23, *Cronquist 8362* (NY,UTC,WS,WTU); **Morrow Co.:** near Lexington, *Leiberg 12* (ORE,US); **Umatilla Co.:** 10 miles E. of Hermiston, *Hills 18* (OSC); **Wasco Co.:** along Columbia River Hwy. E. of The Dalles, *A. & R. Nelson 612* (DS,MO,RM). **Utah. Box Elder Co.:** 12 miles W. of Snowville, *Jensen 137* (UTC). **Washington. Adams Co.:** Ritzville, *Sandberg & Leiberg* 190 (GH,NY,ORE,UC,US,WS); **Benton Co.:** 2 miles N.W. of Richland, *Rose 50092* (CAS,COLO,NY,RSA,UC,US); **Douglas Co.:** Badger Mt., *Thompson 14643* (CAS,DS,GH,MICH,MO,NA,NY,PH,UC,US,WS,WTU); **Franklin Co.:** 1 mile S. of McAdam, *Daubenmire 3839* (WS); **Grant Co.:** 2.9 miles S. of R.R. Bridge on Columbia River near Beverly, *I. & M. Al-Shehbaz 6962* (GH); near Euphrata,

Thompson 6120 (DS,GH,MO,OSC,WTU); **Kittitas Co.:** near Wenatchee, *Whited 1246* (US,WS); **Klickitat Co.:** Bingen, *Suksdorf 8208* (WS); **Walla Walla Co.:** Wallula, *Leckenby s.n.*, 1898 (GH,US,WS); **Yakima Co.:** near Yakima, *Thompson 11315* (CAS, GH,MO,NY,PH,POM,UC,US,WTU).

The most unique feature of *Thelypodium milleflorum*, that is not present in any other species of the genus, is the predominant occurrence of hollow stems that are slightly to moderately inflated above the base. The stems are neither inflated nor hollow in all the other species of *Thelypodium*. There the pith tissue is either solid and continuous throughout or loose to irregularily vacuolated. Older stems are occasionally hollow due to the breaking up of the pith tissue. Over 500 plants of *T. milleflorum* were checked for this feature. All but two were consistently hollow, but there is some variability as to how much of the stem is hollow. In some plants the stem is hollow only to the inflorescence, while in others the rachis and the branches of the inflorescence are hollow for most of their lengths.

The most conspicuous variation in *Thelypodium milleflorum* is in the margin of the basal and lower cauline leaves, and the length and orientation of the siliques. Although the leaf margin tends to be mostly dentate or sinuate, there are varying degrees of transition to pinnately lobed leaves. However, the latter type is rather uncommon, and seems to be restricted to the northern parts of the species range. Basal leaf morphology appears to be less variable in this species than in *T. laciniatum*. The siliques are quite variable in terms of their orientation and length. Such variation can be seen within any sizeable population. The siliques in *T. milleflorum* tend to be erect and somewhat appressed to the rachis, but ascending siliques, that are only appressed or parallel to the rachis near their bases, are by no means uncommon.

The proximal parts of the petioles of the basal leaves are almost always ciliate-margined with simple trichomes. There is considerable variation in the density of these trichomes and in their distribution along the petiole margin. While often restricted to the proximal third of the petioles, they sometimes occur along the petiole margin all the way to the lower part of the leaf blade, or they may be restricted to the very base of the petiole. Unfortunately, such a character is not always easy to observe and it has not been reported for this species or the others that have it, perhaps because the basal leaves in these species are often shed before the plants set flowers or fruits. Despite this, it is usually possible to see these trichomes on the remnants of the petioles, or, in some instances, at the petiole bases of the lowermost cauline leaves.

Thelypodium milleflorum grows predominantly on sandy soils, and it often is associated with sagebrush. It is rather common on sandy dunes in open deserts or along river banks. No other species of *Thelypodium* occurs in this type of habitat.

3. **Thelypodium crispum** Greene ex Payson

Thelypodium crispum Greene ex Pays., Ann. Mo. Bot. Gard. 9:264. 1923. Holotype: Eagle Valley, 1446 m., Ormsby Co., Nevada, June 28, 1902, *C. F. Baker 1191* (RM); isotypes: CAS,GH,MICH,MO,NY,POM,RM,UC,US.

Thelypodiopsis crispa (Greene ex Pays.) O. E. Schulz, Bot. Jahrb. 66: 98. 1933.

Thelypodium brachycarpum Torr. var. *crispum* (Greene ex Pays.) Jeps., Fl. Calif. 2:40. 1936.

Thelypodium leptostachyum Greene, West Am. Pl. 1:19. 1902. This name was a *nomen nudum*, therefore not validly published.

Thelypodiopsis leptostachya (Greene) O. E. Schulz, Bot. Jahrb. 66:98. 1933. This was based on the invalidly published *Thelypodium leptostachyum*, thus the transfer by Schulz also was in error.

Herbaceaus biennial or short lived perennial; stems solid, usually slender, often glaucous, glabrous throughout or sparsely to sometimes densely pilose toward the base, simple or virgately branched at base, with the branches few to several, ascending or subdecumbent, usually branched above, (0.9)1.3–7(12) dm. high; basal leaves thickish, glaucous, glabrous throughout to sparsely pilose, with the trichomes usually most abundant along the petioles and midribs, acute or nearly obtuse at apex, mostly oblanceolate to spatulate, rarely obovate or lanceolate, often pinnately lobed to lyrate, sometimes sinuate or dentate, rarely entire, (1.5)2.2–15(25) cm. long, (0.6)1–3.5(5) cm. wide; lobes entire, linear to oblong or rarely deltoid, acute at apex, remote and narrower on lower part of the leaf, with the divisions between the lobes becoming shallower toward leaf apex; petioles slender, mostly ciliate, (0.7)2–8.5 cm. long; cauline leaves sagittate to auriculate at base, linear to linear-lanceolate or lanceolate, rarely oblong or ovate, usually appressed most of their lengths to the stem and with the upper parts ascending, acute to acuminate at apex, mostly entire, rarely dentate or repand, somewhat glaucous, often glabrous, or sometimes sparsely pilose along midrib or at leaf apex, (0.7)1.2–4.9(8.4) cm. long, (1.5)2–6(13) mm. wide; basal lobes (auricles) mostly lanceolate to deltoid, rarely ovate, acute to obtuse, (0.5)1–6 (11) mm. long, 0.5–2(3.5) mm. wide; inflorescence a densely flowered raceme, sometimes a little lax, elongating slightly in fruit; sepals oblong to linear-oblong, obtuse, somewhat scarious at the margin, greenish above and white below or lavender throughout, often slightly keeled, saccate at the base, (3)3.5–6(8) mm. long, (0.75) 1–1.75(2) mm. wide; petals white or lavender with purplish veins, mostly linear to narrowly oblanceolate, rarely spatulate, often strongly crisped, (6)6.5–11(14.5) mm. long, 0.5–0.75(1) mm. wide; claws 2–4 mm. long; filaments white or rarely lavender, slightly dilated at base, slender, nearly equal in length, (2.5)4.5–8.5(10.5) mm. long; anthers linear to narrowly oblong, apiculate, exserted, sagittate at base, often circinately coiled when fully dehisced, 2–3.5(4.5) mm. long; pistil slender, strongly curved abaxially; glandular tissue only surrounding base of single stamens, sometimes failing to develop beneath them, usually with a lateral extension; fruiting pedicels mostly slender, not flattened at base, erect or ascending-erect, partly or completely appressed to rachis, (1.5)2–5(10) mm. long; siliques terete, torulose, often incurved, sometimes straight, divaricately ascending or occasionally ascending, linear, (0.6)1–2.5(4.2) cm. long, 0.75–1(1.75) mm. wide; styles slender, tapering toward the apex, 0.5–1.5(2.5) mm. long; stigmas entire; gynophores slender, 0.5–1.5(3.5) mm. long; seeds somewhat flattened, 1–1.5(1.75) mm. long; 0.5–0.75(1) mm. wide; cotyledons mostly obliquely incumbent, rarely incumbent.

Flowering from early June to early August in eastern California and adjacent western Nevada (Map 2). The usual altitudinal range of *Thelypodium crispum* is from 4,000 to 8,500 feet, but it has been collected from elevations as high as 10,500 feet near Moat Lake in California (*Smith* 335, CAS). This is the highest known altitudinal limit reached by any species of *Thelypodium*.

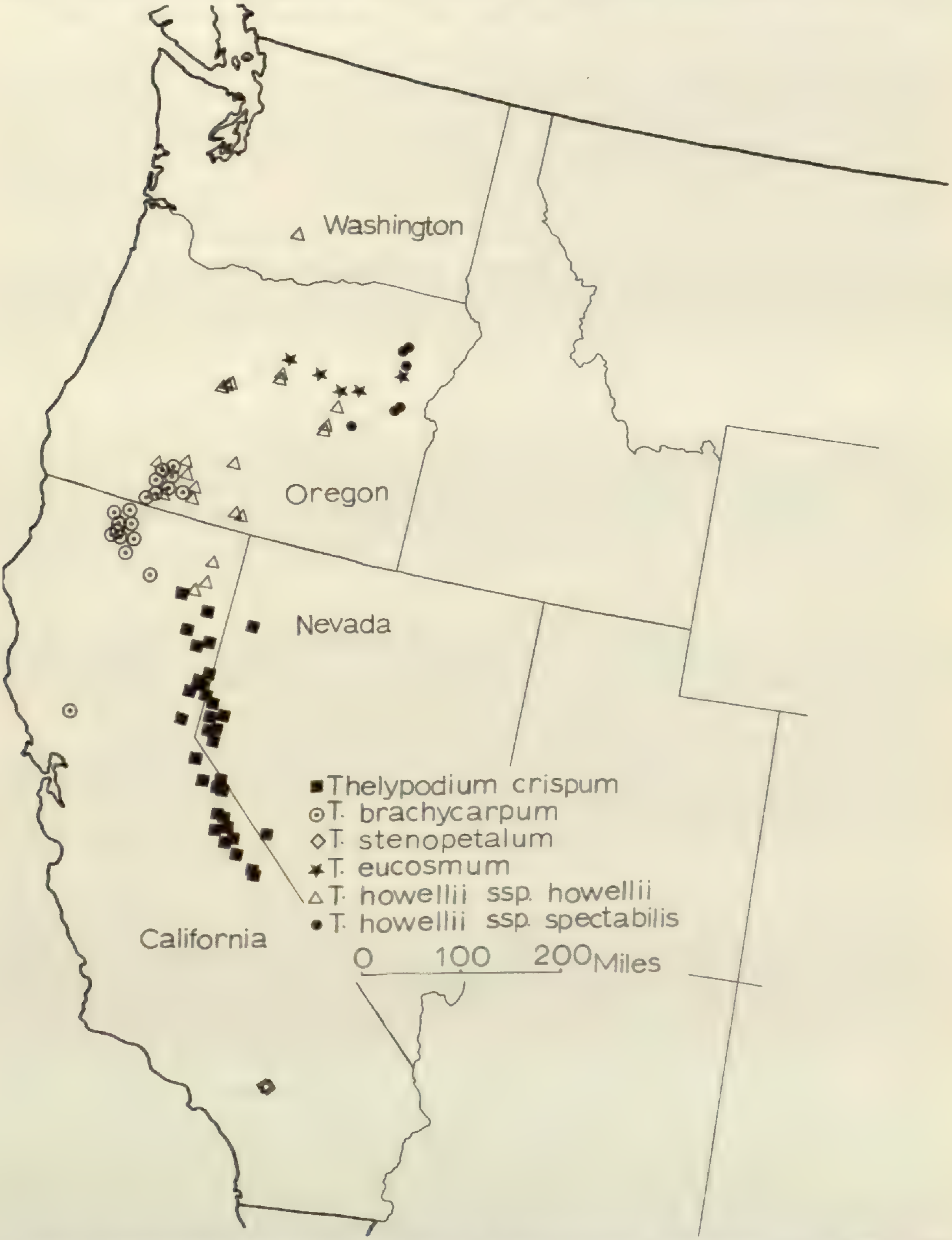
REPRESENTATIVE SPECIMENS. **California. Alpine Co.:** Grover Hot Springs, *I. & M. Al-Shehbaz 6940* (GH); hot springs in Toiyabe National Forest, *Johnson JJ–89* (GH, UTC,WS); **Inyo Co.:** Bishop, *Hall & Chandler 7284* (POM,UC); Hot Creek in Long Valley, *Train s.n.*, 1937 (COLO,DS,NA,POM,UC,US); **Lassen Co.:** 5 miles S. of Ravendale, *Harris 24965* (GH); 3 miles N. of Omira, *Howell 11859* (CAS,F,POM); Milford, *Ripley & Barneby 5684* (CAS,NY); **Mono Co.:** Bodie Creek, *Alexander & Kellogg 4373* (DS, GH,UC,UTC,WTU); Benton Crossing, *I. & M. Al-Shehbaz 68116* (GH); Long Valley, *Howell 14389* (CAS,DS,F,GH,MICH,NY,US,WTU); 1 mile E. of Bridgeport, *Munz 11900* (COLO,DS,NY,RSA,UT,WTU); Gem Lake, *Peirson 6112* (RSA); June Lake, *Rose 40729* (MO,US); below Moat Lake, *Smith 335* (CAS); **Placer Co.:** hot springs at McFarland Mill, *Sonne s.n.*, 1886 (F,UC); **Plumas Co.:** Vinton, *Rose 55149* (CAS,COLO,NY,RSA,UC); **Sierra Co.:** along road to Beckwourth from Calpine, *Bacigalupi, Mason & Sweeney 4283* (JEPS,RSA,WTU); Purdy, *Heller & Kennedy 8671* (CAS,DS,F,GH,MO,NY,UC,US). **Nevada. Douglas Co.:** U.S. Hwy. 50, S. of Carson City, *Delameter s.n.*, 1947 (RSA); **Esmeralda Co.:** Chiatovitch Creek, *Duran 533* (CAS,DS,F,GH,LA,MICH,MO,NY,ORE,RM, RSA,UC,US,UTC,WIS); **Ormsby Co.:** 0.8 mile on hot springs road from U.S. Hwy. 395 at Carson City, *I. & M. Al-Shehbaz 68110* (GH); near Carson City, *Archer 6063* (NA,NY,RSA,TEX,UC,WTU); King's Canon, *Baker 1218* (CAS,GH,MO,ND,NY,POM,RM,UC); **Washoe Co.:** between Washoe and Franktown, *Heller 10598* (DS,GH,NY,US); Washoe Lake, *Jones s.n.*, 1897 (MO,US,UTC); Empire City, *Jones 3769* (CAS,DS,GH,MO,NY,ORE, POM,UC,US,UTC).

Thelypodium crispum has been confused with *T. brachycarpum* for a long time, because the two species are very similar in many morphological features. In their treatment of *T. brachycarpum*, Gray (1865), Greene (1891), and Robinson (1895) stated that this species occurs in western Nevada and eastern California. However, we know that it is restricted to northern California and Oregon, and that the plants from western Nevada and eastern California that were misidentified as *T. brachycarpum* are, in fact, *T. crispum*. *Thelypodium crispum* actually was described by Payson from Baker's collection (no. 1191) that was labelled "*Thelypodium crispum* Greene." The name, therefore, must be written *T. crispum* Greene ex Payson instead of the customarily used *T. crispum* Greene.

Although there is considerable variation in a number of morphological features of *Thelypodium crispum*, the most noticeable is that found in the margin of the basal leaves. The majority of plants have lyrate to pinnately divided leaves, but a number of individuals have the leaves nearly entire to variously dentate. However, such variation is of a continuous nature and usually may be found within the same population. Plate 4 shows the variability in the basal leaves of two population samples. Each leaf was taken from one of the rosettes grown under uniform greenhouse conditions. Cauline leaves are more variable in shape than is their margin. Typically, they are linear to linear-lanceolate with an entire margin, but there are populations with predominately oblong to ovate cauline leaves that are more or less dentate or repand. The latter is particularly true of the populations at Benton Crossing in California. These populations cannot be separated taxonomically, because such characters of the leaves have a sporadic occurrence elsewhere in the species range. As in *T. laciniatum*, the sepals and petals of *T. crispum*

can be white or less often colored, but the flower color does not correlate with any other character nor does it have any geographical basis. Finally, the fruiting pedicels are quite variable in their length, but such variation can easily be seen in any sizeable population.

Thelypodium crispum grows predominantly on loamy to sandy clay soils in meadows or flats of various degrees of alkalinity. It is fairly common on mineralized soils (often disintegrated travertine) in the vicinity of hot springs at a number of localities in eastern California.



Map 2. Distribution of *Thelypodium crispum*, *T. brachycarpum*, *T. eucosmum*, *T. howellii*, and *T. stenopetalum*.

The species most closely related to *Thelypodium crispum* is *T. brachycarpum*. They are so similar to each other in the morphology of their basal and cauline leaves, inflorescences, siliques, and a few features of the flowers that they might be considered conspecific. In fact, Jepson (1936) treated the former species as a variety of the latter. However, the two have been maintained as distinct species by a number of authors since Payson's treatment of *Thelypodium* in 1923. *Thelypodium crispum* is also somewhat related to *T. eucosmum*, which it resembles in some aspects of the flowers, inflorescences, and siliques, but the two are sufficiently different in a number of features that they should only be indirectly associated.

Thelypodium crispum can be easily distinguished from *T. brachycarpum* on the basis of the fruiting pedicels that are erect to ascending, usually slender, not flattened at the base, and with a length of (1.5)2–5(10) mm. In typical *T. brachycarpum* the fruiting pedicels are often horizontal to occasionally divaricate, always stout, flattened at the base, and only 1–2 (2.5) mm. long. From *T. eucosmum, T. crispum* is easily distinguished by its erect or ascending instead of horizontal fruiting pedicels, linear, white instead of oblanceolate, dark purple petals, appressed instead of divaricately ascending leaves, shorter siliques, and narrower divided basal leaves.

4. Thelypodium brachycarpum Torrey

Thelypodium brachycarpum Torr., Bot. U.S. Expl. Exped., Plate 1, 1862; Wilkes' Expl. Exped. 17:231. 1874. Holotype: Wilkes' Expedition, between Clamet and San Francisco, no. 1596 (US). Two specimens of the Wilkes' Expedition were seen by the present writer. The one in Torrey's Herbarium (at NY) was labelled "*Thelypodium brachycarpum*, southern Oregon" and is made up of a few fragmentary branches. This is not the type. The second specimen (US) is without question the type because it corresponds very well with the original plate published in 1862, and it is labelled as being the basis for the plate of "*Pachypodium brachycarpum.*"

Thelypodiopsis brachycarpa (Torr.) O. E. Schulz. Bot. Jahrb. 66:98. 1933.

Thelypodiopsis brachypoda O. E. Schulz, Bot. Jahr. 66:98. 1933. Holotype: Shasta Valley, alt. 3,000 feet, Siskiyou Co., California, June 1903, *H. M. Hall & E. B. Babcock 4092* (not seen); isotypes: MO,NY,UC,US.

Plants tap rooted biennials; stems solid, stoutish to slender, erect, simple or virgately branched from the base, usually branched above, somewhat glaucous, glabrous throughout or sparsely to densely pubescent near the base, rarely pubescent to the inflorescence, (1.3)3.4–8.3(12) dm. high, trichomes simple, often long and spreading; basal leaves thickish, glaucous, glabrous or sparsely to densely hirsute, with the trichomes usually most abundant along petioles and midribs, mostly spatulate or oblanceolate, sometimes lanceolate or rarely obovate to elliptic, pinnately lobed to lyrate, occasionally sinuate to dentate, rarely repand or entire, often attenuate at base, 3.3–14(20) cm. long, (0.5)1–3.2(4.7) cm. wide; lobes often oblong, entire, acute to obtuse, remote and narrower on lower part of leaf; petioles slender, glabrous or pubescent, (1.5)2–5.2(9) cm. long; cauline leaves mostly linear to lanceolate-linear, or lanceolate, acute to acuminate at apex, entire, sagittate at base, glaucous and often glabrous, sometimes slightly appressed to stem, gradually reduced upwards, with the uppermost leaves usually ovate-lanceolate, (1)2–6.4(8.7) cm. long, (2) 3–9.3(12.5) mm. wide; basal lobes lanceolate or sometimes ovate, acute to obtuse, (1)3–10(15) mm. long, (0.5)1–3(5) mm. wide; inflorescence a densely flowered raceme, slightly elongated in fruit; sepals lanceolate to linear-lanceolate or

ovate, somewhat scarious at margin, often acuminate, erect, slightly saccate at base, white, often with a prominant midvein, slightly keeled, median (outer) sepals slightly inserted above the lateral ones, (3) 3.5–5(5.5) mm. long, 1–1.5(2) mm. wide; petals linear to narrowly oblanceolate, often crisped, white, 8–12.5(16) mm. long, 0.3–0.5(1) mm. wide, claws erect, narrow, thickish, 2.5–4 mm. long; filaments white, slender, erect, slightly dilated at base, nearly equal in length or slightly tetradynamous, (2)2.5–6.5(10) mm. long; anthers sagittate at base, often strongly apiculate, linear to narrowly oblong, exserted, somewhat circinately coiled when fully dehisced, (1)1.5–2(2.5) mm. long; glandular tissue flat, surrounding the base of single stamens, well-developed above the base, often undeveloped beneath, usually with a lateral extension on each side, median tissue absent; fruiting pedicels stout, mostly flattened at base, horizontal to somewhat divaricate, straight or sometimes slightly curved upwards, 1–2(2.5) mm. long; siliques linear, terete, torulose, straight to curved, divaricately ascending to somewhat divaricate, (0.8)1.2–2.7(3) cm. long 1–1.5(2) mm. wide; styles slender, tapering to the stigma, (0.25)0.5–1(2) mm. long; stigmas entire; gynophores slender, (0.5)1–2(5) mm. long; seeds plump, (1.3)1.5–2 mm. long, (0.75)1(1.25) mm. wide; cotyledons obliquely incumbent or sometimes incumbent.

Flowering mid April to late August, but mainly late May through July, at elevations from 2,000 to 7,500 feet in northern California and southern Oregon (Map 2).

REPRESENTATIVE SPECIMENS. **California. Napa Co.:** just W. of Knoxville on Lower Lake-Knoxville Road, *Rattenbury s.n.*, 1949 (UC); **Shasta Co.:** Pitt River, *Smith 305* (CAS,US); **Siskiyou Co.:** 8 miles W. of jct. California roads 139 and 161, near Lower Klamath Lake, *I. & M. Al-Shehbaz 68139* (GH); 3.8 miles S.E. of Gazelle on U.S. Hwy. 99, near railroad tracks, *I. & M. Al-Shehbaz 6949* (GH); N. side of Mt. Shasta, *Brown 469* (MO,NY,UC,US); Montague, *Heller 8011* (CAS,DS,F,GH,MO,NY,PH,UC); N. end of Shasta Valley near Klamath River, *Heller* 14441 (CAS,COLO,DS,F,GH,LA,MICH,MO, NY,ORE,PH,RM,RSA,UC,WS,WTU); Yreka, *Parker s.n.*, 1948 (DS,GH,RM,RSA,UC,UTC,WS, WTU); Weed, *Smith 285* (CAS); 3 miles S. of Grenada, *Wheeler 3637* (GH,MO,NA,ND, NY,POM). **Oregon. Klamath Co.:** Harriman Lodge Station, *Abrams 9724* (DS,MO, POM,RM); near Dairy, *Applegate 42* (DS,GH,US); near mouth of Williamson River, *Coville 1241* (US); Modoc Point, *Evans 340* (ORE,PH); 1 miles S.E. of Keno, *Peck 9401* (GH,MO,NY,WS).

In his original description of *Thelypodiopsis brachypoda*, Schulz (1933) gave the following description for the new species: "Pedicelli 0.5 mm. longi. Flores parvi." Later (1936, p. 583), he distinguished this species from *Thelypodiopsis brachycarpa* by giving pedicels 0.5 instead of 1.5 mm. long. The four isotypes of the former "species" that I have studied are indistinguishable from plants of *Thelypodium brachycarpum* in every morphological aspect. Moreover, the pedicels in these four isotypes are 1–2 mm. long. The placement of this species and its close relatives in *Thelypodiopsis* by Schulz (1933, 1936) has been discussed previously under generic relationships.

The single collection from Napa County cited here is somewhat disjunct from the main distribution center of the species. Whether this disjunction is the result of a recent introduction by man or possibly an old relict population is not known.

There is relatively little variation in most of the morphological features in *Thelypodium brachycarpum*. Fruiting pedicels seem to vary

only a little in length. The most conspicuous variation is in the margin and the degree of pubescence of basal leaves. This is similar to the variation found in *T. crispum*.

Thelypodium brachycarpum grows primarily in meadows and open flats with varying degrees of alkalinity. It can tolerate highly alkaline soils where it was found either growing by itself or at least more abundantly than any other plant species in the most alkaline parts of a given meadow. In this respect, it resembles *T. crispum*, which occupies somewhat similar habitats in eastern California and western Nevada.

5. Thelypodium eucosmum Robinson

Thelypodium eucosmum Robins. in Gray, Synop. Fl. N. Am. 1:175. 1895. Holotype: Baker City, Baker Co., Oregon, *R. D. Nevius s.n.*, 1875 (GH).

Herbaceous biennial or short-lived perennial by rootstock; stems solid, slender, simple or branched near the base, always branched above, glabrous and somewhat glaucous throughout, often purple colored, 2–10.1 dm. high; basal leaves mostly oblong to lanceolate or oblanceolate, sometimes elliptic to ovate, acute at apex, cuneate or sometimes attenuate at base, entire to occasionally repand or sinuate, glabrous and somewhat glaucous, (2.8)3.5–8.8(11.1) cm. long; (0.7)1–2.5(3.5) mm. wide; petioles slender, usually purple, ciliate near the base, with trichomes simple and straight, (0.9)1.4–3.1(4.5) cm. long; cauline leaves lanceolate to oblong-lanceolate or oblong, acute to obtuse at apex, entire, often cordate-clasping to strongly auriculate at the base, ascending, glabrous and glaucous, 1.8–4.5(6) cm. long, 0.5–1.6(2.4) cm. wide; basal lobes ovate, obtuse, (2.5)3.5–7(8.5) mm. long, nearly as wide; inflorescence somewhat densely flowered raceme, slightly elongated in fruit; floral buds purple, oblong-linear; sepals lilac-purple, equal at base, not saccate, obtuse, somewhat scarious at margin, 5–7(8) mm. long, (0.75)1–1.5(1.75) mm. wide; petals dark purple, mostly spatulate to oblanceolate, obtuse, entire to somewhat repand, attenuate at base, (6.5)7.5–10(11.5) mm. long, 1–1.75(2) mm. wide; claws slender, nearly erect, (3)3.5–5(5.5) mm. long; filaments slender, purplish, erect below and somewhat recurved above, nearly equal in length, (4.5)6–9(10) mm. long; anthers linear to narrowly oblong, sagittate at base, purplish, well exserted, circinately coiled when fully dehisced, 2.5–4(4.5) mm. long; glandular tissue disc-like, surrounding base of single stamens, more developed above the base than below, subtending base of paired stamens; fruiting pedicels slender, mostly straight or rarely curved, more or less flattened at base, horizontal to divaricate, (2.5)3–5.5(6.5) mm. long; siliques narrowly linear, terete, torulose, straight to somewhat incurved, divaricate to ascending, (2)2.4–5(6.5) cm. long, 0.75–1(1.25) mm. wide; styles cylindrical to rarely subclavate, 0.5–1.5(2) mm. long; stigmas entire; gynophores (1)2.5–6(7.5) mm. long; seeds 0.75–1.5 mm. long, 0.5–0.75 mm. wide; cotyledons often obliquely incumbent or rarely incumbent.

Flowering May to July in central and eastern Oregon. *Thelypodium eucosmum* was said to be present in Idaho by Rydberg (1917, 1923), Peck (1941, 1961), and Davis (1952). However, I have seen no specimens of this species from Idaho, and it seems unlikely that it grows outside of Oregon.

REPRESENTATIVE SPECIMENS. **Oregon. Baker Co.:** Blue Mountains, Fox Valley, *Griffiths & Hunter 142* (NY,UC); Blue Mountains, *Howell 345* (GH); **Grant Co.:** Canyon City, *Howell s.n.*, 1885 (F,NA,NY,ORE,PH,UC,US); moist ground along John Day River, 15 miles above Dayville, *Peck 16035* (DS,WTU); 17 miles E. of Prairie City,

Peck 16035 (NY); **Wheeler Co.:** Sutton Mountain, 10 miles N. of Mitchell in T. 10S., R. 21 E., S. 29, *Cronquist 7249* (CAS,DS,GH,MO,NY,OSC,RM,RSA,UC,UTC,WS,WTU); same locality, *Al-Shehbaz & Cronquist 6972* (GH).

Thelypodium eucosmum is the prettiest species in the genus because of its bright purple flowers. However, it appears to be very rare, as judged from the very few collections that exist in the major herbaria of this country. Two different observations have been made with regard to the habitat where *T. eucosmum* grows. The present writer and Dr. Cronquist collected it from shady places under the junipers on one of the dry slopes of Sutton Mountain, while Peck collected it from moist ground along John Day River.

Thelypodium eucosmum does not appear to be very closely related to any other species. It stands as morphologically intermediate between the previous four species and most of the remaining auriculate-leaved species. Payson (1923) considered *T. eucosmum* the most primitive species of the genus, but the evidence at hand indicates that this is not the case. The relationships of *T. eucosmum* to the rest of the species were discussed above under the section on evolution within the genus.

The combination of the following characters easily distinguishes *Thelypodium eucosmum* from the other species of the genus: long gynophores, dark purple flowers arranged in a raceme, exserted anthers, and oblong-linear floral buds.

6. **Thelypodium rollinsii** Al-Shehbaz, sp. nov.

Herba biennis; caulibus erectis, tenuibus farctis, simplicibus ad basin et superne ramosis, (4)6–16(20) dm. altis, foliis radicalibus petiolatis, crassis, glabris et glaucis, spathulatis vel oblanceolatis, dentatis vel repandis, 1.3–4(7) cm. longis, (0.4)0.6–1.3(1.8) cm. latis; foliis caulinis auriculatis, linearibus vel lineari-lanceolatis, acutis vel acuminatis, ad caulem appressis, (0.8)1.3–4.5(6.1) cm. longis, (1)1.7–7(8) mm. latis; auriculis 0.5–2.5(5) mm. longis, 0.5–1.5(2.5) mm. latis; sepalis linearibus vel oblongo-linearibus, erectis, lavandulis vel purpureis, non saccatis, ad marginem scariosis, 4–6(7) mm. longis, 0.75–1(1.5) mm. latis; petalis erectis, spathulatis vel obovatis, non crispis, lavandulis vel purpureis, (6)7–9.5(12) mm. longis, (1.2)1.5–2(3) mm. latis, unguibus 3–4.5(5.5) mm. longis; staminibus erectic, filamentis lateralibus (4)5–6.5(7.5) mm. longis, filamentis medianis (5)5.5–7.5(8.5) mm. longis; antheris exsertis, linearibus vel oblongo-linearibus, non apiculatis, sagittatis, introrsis, circinatibus post dehiscentiam, 2–3(4) mm. longis; infructescentibus congestis (1)2–10.5(18) cm. longis; pedicellis fructiferis tenuibus, striatis, rectis, divaricatis vel horizontalibus, non complanatis, (6)7–14(18) mm. longis; siliquis stipitatis, teretibus, tenuibus, torulosis, valde incurvatis, (1.8)2.8–5.0(6.3) cm. longis, 0.75(1) mm. latis; stipite 0.5–2.5(6) mm. longo; stylis (0.5)0.75–1.5(2) mm. longis; stigmatibus parvis, integris; seminibus uniseriatis, oblongis, exalatis; cotyledonibus oblique incumbentibus.

Holotype in the Gray Herbarium, collected on alkalaine soil in the vicinity of Sevier River, about 12 miles north of Scipio on U.S. Hwy. 91, Juab County, Utah, July 29, 1969, *Ihsan A. & Mona M. Al-Shehbaz 6913;* isotypes to be distributed.

Plant herbaceous biennial, glabrous and somewhat glaucous throughout; stems erect, often slender, solid, single from the base, branched at the inflorescence, (4)6–16(20) dm. high; basal leaves thickish, spatulate or less often oblanceolate to obovate, obtuse to sometimes acute at apex, dentate or repand, very rarely entire, mostly attenuate at

base, 1.3–4(7) cm. long, (0.4)0.6–1.3(1.8) cm. wide; petioles slightly expanded at base, glabrous, 0.5–1.3(1.5) cm. long; cauline leaves mostly linear to lanceolate-linear, acute to acuminate below, mostly acuminate above, auriculate to occasionally sagittate at base, entire, partly to more often completely appressed to stem, becoming greatly reduced on the lateral branches of the inflorescence and usually non-auriculate, (0.8)1.3–4.5(6.1) cm. long, (1)1.7–7(8) mm. wide; auricles tooth-like, acute to obtuse, 0.5–2.5(5) mm. long, 0.5–1.5(2.5) mm. wide; inflorescence corymbose, somewhat densely flowered, often slightly elongated in fruit; sepals linear to oblong-linear or sometimes oblong, obtuse, scarious at margin, purple to lavender throughout, or lavender at the margin and green in the center, equal at base, sometimes slightly saccate, erect, 4–6(7) mm. long, 0.75–1(1.5) mm. wide, sepals often with a somewhat prominant midvein; petals not crisped, lavender to purple, obtuse to rarely acutish, with the blade spatulate to oblong or obovate, (6)7–9.5(12) mm. long, (1.2)1.5–2(3) mm. wide; claws erect, slender, 3–4.5(5.5) mm. long; filaments slender, terete, slightly tetradynamous, often lavender, erect, filaments of paired stamens (5)5.5–7.5(8.5) mm. long, filaments of single stamens (4)5–6.5(7.5) mm. long; anthers exserted, linear to oblong-linear, sagittate at base, often lavender or purple, 2–3(4) mm. long; glandular tissue well-developed around the base of single stamens, narrower and subtending base of paired stamens; infructescence congested, (1)2–10.5(18) cm. long; fruiting pedicels straight, slender, striate, mostly divaricate to horizontal, rarely divaricately ascending, mostly not flattened at the base, (6)7–14(18) mm. long, 0.25–0.5 mm. wide; siliques glabrous, slender, terete, somewhat torulose, often strongly incurved, with the distal ends mostly erect, rarely straight and divaricately ascending, (1.8)2.8–5.0(6.3) cm. long, 0.75(1) mm. wide; styles slender, (0.5)0.75–1.5(2) mm. long; stigmas entire; gynophores 0.5–2.5(6) mm. long, usually slender; seeds 1–1.3(1.5) mm. long, 0.5–0.6(0.75) mm. wide; cotyledons oblique, rarely incumbent.

Flowering late June through mid August at elevations from 5,000 to 6,500 feet in central Utah.

REPRESENTATIVE SPECIMENS. **Utah. Carbon Co.:** 15 miles E. of Wellington, *Malburtt s.n.*, 1959 (UT,UTC); **Juab Co.:** 14.5 miles S.W. of Levan on U.S. Hwy. 91, *I. & M. Al-Shehbaz* 6979 (GH); 9 miles S.W. of jct. U.S. Hwy. 91 and Utah State Hwy. 28, *I. & M. Al-Shehbaz* 6981 (GH); ca. 10 miles N. of Scipio along U.S. Hwy. 91, *Higgins* 1794 (GH); **Millard Co.:** 32 miles N. of Filmore, *Holmgren & Tillett* 9654 (CAS,GH,MO,NY,UC,US,UTC,WS,WTU); **Piute Co.:** ca. ½ mile S. of Piute-Sevier County line on U.S. Hwy. 89, *I. & M. Al-Shehbaz* 6910 (GH); Marysvale, *Jones* 5965B (NY, POM,US); along Sevier River above Marysvale, *Rydberg & Carlton* 6926 (GH,NY,RM,US); **Sanpete Co.:** ca. 2 miles S. of Sterling on U.S. Hwy. 89, Nine-Mile Reservoir, *I. & M. Al-Shehbaz* 6907 (GH); same locality *I. & M. Al-Shehbaz* 6982 (GH); Manti, *Jones* 5521 (NY); **Sevier Co.:** 0.1–0.2 mile S. of Redmond, *I. & M. Al-Shehbaz* 6908 (GH); same locality, *I. & M. Al-Shehbaz* 6983 (GH); 1.6 miles S.W. of Salina on U.S. Hwy. 89 at Sevier River, *I. & M. Al-Shehbaz* 6909 (GH).

Thelypodium rollinsii is an abundant species on the alkaline flats along the Sevier River and adjacent areas in central Utah. However, it is surprising to find very few collections of it in the major herbaria of this country. More surprising is the fact that some specimens of this species were available to taxonomists such as Rydberg, Jones, and Payson, who, for one reason or another, failed to describe it. In fact, Payson (1923) cited the only collection that he saw (Rydberg & Carlton 6926, RM) under *T. lilacinum*, while others have misidentiified it as *T. saggittatum*.

There is some variability among the specimens cited above. This applies

especially to certain features such as the size of the auricles, length of the fruiting pedicels and infructescences, and the color of the flowers.

The closest relative to *Thelypodium rollinsii* is *T. integrifolium*, which it resembles in habit and several features of the flowers. The new species is morphologically intermediate between *T. integrifolium* and *T. sagittatum* in a number of features, but it is quite different from either one in the nature of its fruiting pedicels, cauline and basal leaves, and siliques. It is also very different in its mustard oils as we have shown above.

Thelypodium rollinsii can be easily distingushed from its nearest relative, *T. integrifolium*, by the following characteristics: the basal leaves are very small, 1.3–4(7) cm. long, (0.4)0.6–1.3(1.8) cm. wide, often dentate or repand (Plates 3 and 19). The cauline leaves are almost always auriculate and partly to completely appressed to the stem (Plate 17). The calyx is somewhat 4-sided, and median glandular tissue is present (Plate 18). The fruiting pedicels are slender, (6)7–14(18) mm. long, and often not flattened at base. Finally, the siliques are slender, often strongly curved, and 0.75(1) mm. wide (Plate 20). In *T. integrifolium*, as represented by its five subspecies, the basal leaves are (3.7)5–31(54) cm. long, (1.2)1.6–7.8(14) cm. wide, often entire (Plates 3 and 19). The cauline leaves are not appressed to the stem (Plate 17), but they are usually ascending, sessile and without auricles (reduced auricles were found in 8 plants out of more than one thousand studied). The median glandular tissue is absent (Plate 18). Fruiting pedicels are slender to stout, mostly flattened at the base, (2)3–9(13) mm. long. The siliques are slender to stout, straight or curved, 1–1.3(2) mm. wide. *Thelypodium rollinsii* is distinguished from *T. sagittatum* by its glabrous instead of ciliate basal leaf petioles, smaller and dentate instead of the larger and entire basal leaves, its appressed instead of ascending cauline leaves, its branching habit, exserted stamens, longer stems, and inflorescences that are hardly elongated in fruit.

7. **Thelypodium integrifolium** (Nuttall) Endlicher

Herbaceous biennial; stems often simple or sometimes branched at base, corymbosely or somewhat paniculately branched at the inflorescence, slender to stout, purple to whitish green, glabrous and somewhat glaucous throughout, (2)4.5–17(28) dm. high; basal leaves thickish, glabrous and somewhat glaucous, mostly oblong or elliptic to oblanceolate, sometimes spatulate to lanceolate, rarely ovate or obovate, mostly entire, occasionally denticulate or repand, obtuse to less often acute at apex, cuneate to sometimes attenuate at base, earlier leaves usually broader and with longer petioles than later ones, (3.7)5–31(54) cm. long, (1.2)1.6–7.8(14) cm. wide; petioles glabrous, expanded at base, (0.5)1.2–10(15) cm. long; cauline leaves thickish, glabrous, slightly to moderately glaucous, obtuse to more often acute or acuminate, entire or rarely denticulate, mostly ascending, seldom minutely auriculate, lower cauline leaves mostly oblanceolate to lanceolate, upper leaves linear-lanceolate to linear, sessile, (1)2.2–8.3(19.5) cm. long, (1.5)2.5–11(25) mm. wide; inflorescence corymbose or very short racemose, somewhat densely flowered; sepals linear-oblong to linear, erect, obtuse, somewhat scarious at margin, greenish above and creamy

white to lavender below, or lavender to dark purple throughout, equal at base, the lateral sepals sometimes slightly saccate, glabrous, (3)3.5–5.5(7.5) mm. long, (0.5)0.75–1(1.5) mm. wide; petals oblanceolate to spatulate, not crisped, obtuse, white to lavender or dark purple, erect, (4.5)6–9(13) mm. long, (0.5)0.75–1.5(2.3) mm. wide; claws (2)3–4.5(7) mm. long; filaments slender, erect, white to lavender or purple, nearly equal or somewhat tetradynamous, (3)4.5–7.5(12.5) mm. long; anthers exserted, linear to narrowly oblong, sagittate at base, purple to lavender, (1)1.5–2.5(4.5) mm. long; median nectar glands absent, lateral glands well-developed above base of lateral stamens, open or emarginate, absent or reduced below, glands flat, bilobed or with two strongly developed tooth-like processes that rarely exceed 1 mm. in length; infructescence racemose or subumbellate, (0.6)1.5–14.5(28) cm. long, lax to congested; fruiting pedicels slender to stout, straight or rarely curved, horizontal to divaricate, rarely ascending or reflexed, somewhat striate at least near the tip, glabrous and sometimes glaucous, strongly to moderately flattened at base, or sometimes not flattened, (2)3–9(13) mm. long; siliques terete to somewhat flattened, torulose or rarely submoniliform, straight to more often strongly incurved, divaricate to divaricately ascending or horizontal, rarely reflexed (0.7)1.3–3.4(8.0) cm. long, 1–1.3(2) mm. wide; styles slender, tapering toward the tip, rarely subclavate, 0.5–1.3(3.2) mm. long; stigmas entire; gynophores slender, (0.3)0.5–2(5.5) mm. long; seeds (1)1.2–2(2.3) mm. long, 0.75–1(1.25) mm. wide; cotyledons obliquely incumbent or rarely incumbent.

PLATE 17. Cauline leaves of *Thelypodium integrifolium* (FIG. 1) and *T. rollinsii* (FIG. 2). Natural size.

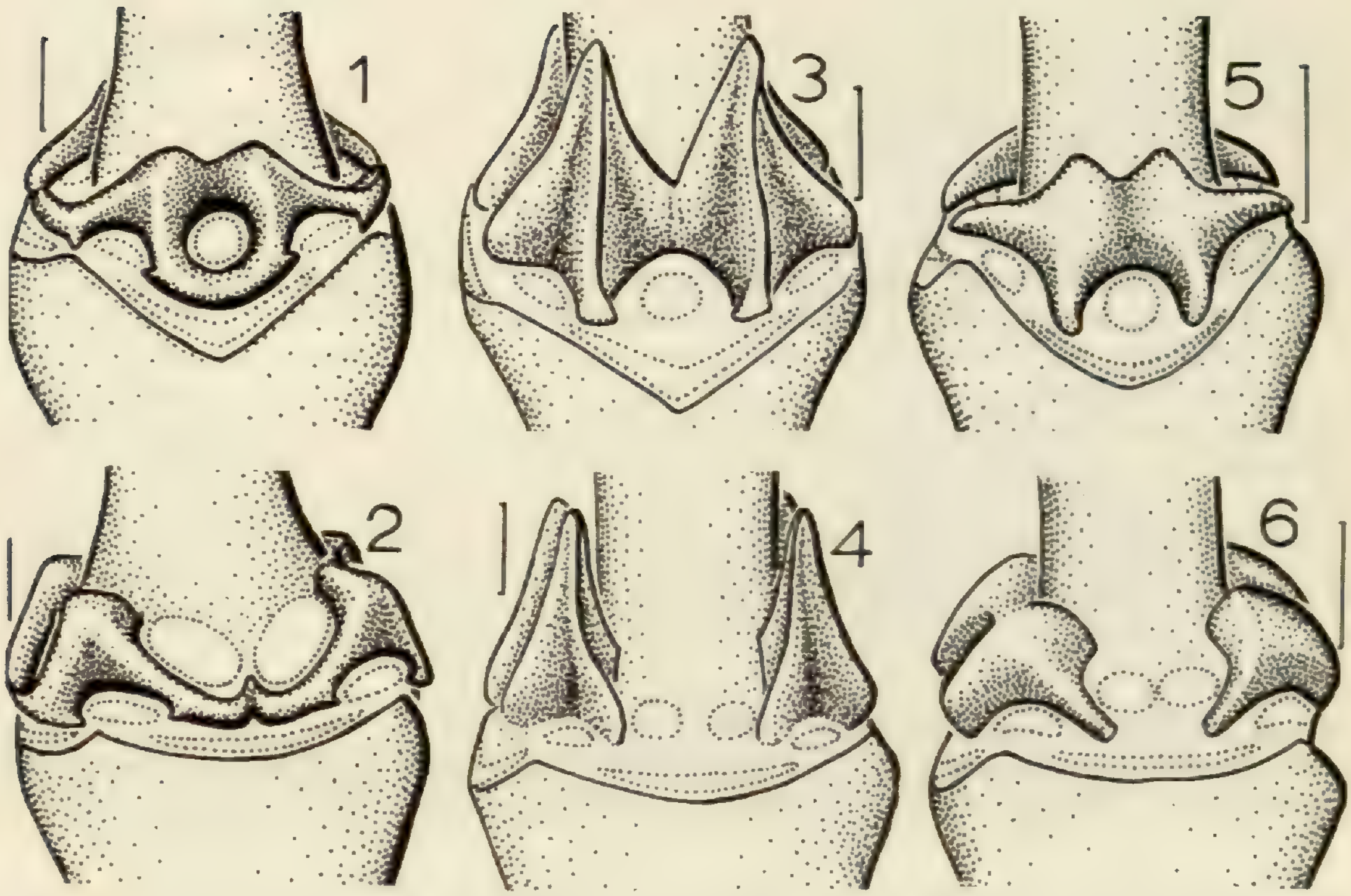


PLATE 18. Nectar glands of *Thelypodium rollinsii* and *T. integrifolium*. Figs. 1, 2. *T. rollinsii*; FIGS. 3–6. *T. integrifolium*. Figures 1, 3, 5 lateral view; 2, 4, 6 median view. Scale ½ mm.

KEY TO THE SUBSPECIES

A. Flowers white; mature fruiting pedicels stout, whitish, 6–13 mm. long.
  B. Siliques (2.2)3.5–6.3(8.0) cm. long; fruiting pedicels (6)7–11(13) mm. long, horizontal to divaricate or reflexed; gynophores (1)1.5–4(5.5) mm. long; petals (7.5)8–11(13) mm. long; plants of the Grand Canyon of the Colorado River in Arizona ..... 7e. subsp. *longicarpum*.
  B. Siliques (1.4)1.9–3.7(4.5) cm. long; fruiting pedicels (5)6–9(13) mm. long, horizontal to divaricate; gynophores (0.5)1–3 mm. long; petals (5)6–9(10) mm. long; plants of southeastern California, southern Nevada, and southwestern Utah ..... 7d. subsp. *affine*.
A. Flowers lavender to purple or sometimes white; mature fruiting pedicels not whitish, 2–13 mm. long, slender, or if stout, then 2–5(6) mm. long.
  C. Mature fruiting pedicels mostly stout, 2–5(6) mm. long, strongly flattened at base.
    D. Infructescence long raceme, somewhat congested, central rachis (3)8–20(28) cm. long; gynophores slender (0.5)0.75–3(4) mm. long; plants of eastern Utah, western Colorado, northwestern New Mexico, and northeastern Arizona ..... 7c. subsp. *gracilipes*.
    D. Infructescence short raceme, often strongly congested, central rachis (0.6)1.2–7(9) cm. long; gynophores stout, 0.5–1(3) mm. long; plants of northwestern Utah, Nevada, eastern California, and southern Oregon ..... 7b. subsp. *complanatum*.
  C. Mature fruiting pedicels often slender and somewhat flattened at the base, or stout and not flattened, 6–13 mm. long, rarely shorter and not flattened at base, sometimes infructescence strongly subumbellate; widely distributed ..... 7a. subsp. *integrifolium*.

7a. **Thelypodium integrifolium** (Nuttall) Endlicher subsp. **integrifolium**

Pachypodium integrifolium Nutt. in Torr. & Gray, Fl. N. Am. 1:96. 1838. Holotype: "Elevated plains of the Rocky Mountains, towards the Oregon, as far as Wallawallah," *Nuttall s.n.* (not seen); isotypes: GH,NY.

Thelypodium integrifolium (Nutt.) Endl. Walp. Repert. 1:172. 1842.

Pleurophragma integrifolium (Nutt.) Rydb., Bull. Torr. Bot. Club 34: 433. 1907.

Thelypodium lilacinum Greene, Pl. Baker. 3:9. 1901. Holotype: Doyle's, alt. 8,100 feet, July 29, 1901, *C. F. Baker* 635 (ND–G); isotypes: GH,MO,NY,POM,US.

Pleurophragma lilacinum (Greene) Rydb., Brittonia 1:89. 1931.

Thelypodium lilacinum Greene var. *subumbellatum* Pays., Ann. Mo. Bot. Gard. 9:281. 1923. Holotype: near Mammoth Hot Springs, Yellowstone National Park, Wyoming, alt. 6,200 feet, August 1893, *F. H. Burglehaus s.n.* (MO); isotypes: MICH, US,TU.

Flowers lavender to purple or rarely white; petals (4.5)5.5–8(10.5) mm. long; infructescence racemose to subumbellate, congested to somewhat lax, central rachis (0.5)1.2–10(25) cm. long; fruiting pedicels mostly slender or sometimes stoutish, straight to slightly curved upwards, mostly divaricate to divaricately ascending, rarely horizontal, slightly flattened or not at base, (4)5–10(13) mm. long; siliques straight to incurved, divaricately ascending to ascending, (1.0)1.5–3.0(4.1) cm. long; gynophores stout, 0.5–1.2(2.5) mm. long; glandular tissue flat and low, bilobed or with two strongly developed tooth-like processes that are free to variously united.

Flowering from early June to late September, but mainly late June through August, at elevations from 2,000 to 8,100 feet. Distributed in central Washington, Oregon, Idaho, southwestern Montana, Wyoming, central and northern Utah, northern and central Colorado, western Nebraska, western South Dakota, and central North Dakota (Map 3).

REPRESENTATIVE SPECIMENS. **Colorado. Eagle Co.:** about 20 miles N.E. of Glenwood Springs, *Rollins 1887* (DS,GH,MO,ND,NY,US,WS); **Fremont Co.:** Wet Mt. Valley, *Brandegee 821* (MO,NY,PH,UC); **Grand Co.:** Hot Sulphur Spring, *Nelson 9777* (GH, MO,RM,UC); **Gunnison Co.:** Cebolla Hot Springs, Powderhorn, *I. & M. Al-Shehbaz 6903 & 6995* (GH); **Larimer Co.:** 1 mile W. of La Porte, *Ginter 679* (NA); **Weld Co.:** Roggen, *Weber 5944* (COLO). **Idaho. Bear Lake Co.:** 2 miles E. of St. Charles, *Christ 18669* (NY); **Bingham Co.:** Springfield, *Christ 8944* (NY); **Butte Co.:** 11.2 miles N.W. of Howe, *I. & M. Al-Shehbaz 6920* (GH); **Canyon Co.:** 4.4 miles N.W. of Notus on U.S. Hwy. 26, *I. & M. Al-Shehbaz 6973* (GH); **Caribou Co.:** 1 mile E. of Soda Springs, *Christ 16167* (NY); **Cassia Co.:** 23 miles E. of Rupert, *J. & C. Christ 18541* (NY); **Custer Co.:** Clayton, *Macbride & Payson 3360* (CAS,DS,GH,MO,NY,POM,RM,UC,US); **Elmore Co.:** near King Hill, *Nelson & Macbride s.n.*, 1911 (RM); **Lemhi Co.:** Salmon, *Henderson 3881* (US); **Power Co.:** American Falls, *Nelson & Macbride 1380* (DS,F, GH,MO,NY,POM,RM,UC,US,UTC,WS,WTU); **Twin Falls Co.:** Twin Falls & Shoshone Falls, *Nelson & Macbride 1349* (DS,F,GH,MO,RM). **Montana. Deer Lodge Co.:** Deep Creek near Anaconda, *Jones s.n.*, 1905 (MO,ORE,POM,US); **Gallatin Co.:** Three Forks, *Blankinship 23* (MO,NMC,POM,RM,UC); **Lewis & Clark Co.:** Helena, *Kelsey s.n.*, 1891 (DS,F,POM); **Wheatland Co.:** Musselshell River Bottom, 4 miles E. of Shawmut, *Hitchcock 2424* (RSA). **Nebraska. Banner Co.:** Upper Pumpkin Seed Creek, *Rydberg 13* (NY,US); **Morrill Co.:** Bridgeport, *Baker s.n.*, 1901 (MO). **North Dakota. Burleigh Co.:** Baldwin, *Stevens 711* (GH,UC,US); **Kidder Co.:** near Lake Tappen, *Stevens s.n.*, 1919 (F,NY); **McLean Co.:** Fort Berthold Reservation, *Heidenreich 236* (NA); **Ward Co.:** Ryder, *Stevens s.n.*, 1923 (MO). **Oregon. Crook Co.:** near Prineville, *Leiburg 817* (DS,F,GH,JEPS,MO,NY,ORE,POM,UC,US); **Harney Co.:** Stein's Mountain, *Train s.n.*, 1935 (OSC); **Lake Co.:** Johnson Creek, Summer Lake, *Constance 9542* (PH); **Malheur Co.:** Crooked Creek, *Train s.n.* (US). **South Dakota. Custer Co.:** Pringle, *Over 15957* (RM,

US); **Pennington Co.:** Rapid Creek, Rapid City, *McIntosh 209* (RM). **Utah. Cache Co.:** 1 mile W. of Logan, *Smith 2003* (CAS,DS,RM,UTC); **Piute Co.:** ca. 7 miles W. of Junction, up City Creek Canyon along Hwy. 153, *Higgins 1796* (GH); **Rich Co.:** near Bear Lake, *Garrett 7461* (DS,GH); **Salt Lake Co.:** Murray, *Jones 407* (GH); **Sanpete Co.:** Ephraim, *Jones 5522* (DS,MO,POM); **Utah Co.:** Provo, *Jones 5496* (US); **Wasatch Co.:** near Midway, *Carlton & Garrett 6705* (NY,RM,US). **Washington. Douglas Co.:** below Dry Falls, Grand Coulee, *Kruckeberg 2807* (COLO,RSA,WS,WTU); **Grant Co.:** 8.5 miles S.W. of Sun Lake State Park entrance on Washington Hwy. 17, *I. & M. Al-Shehbaz 6967* (GH); Dry Falls, *Thompson 11816* (CAS,DS,MO,NY,WS,WTU); **Kittitas Co.:** near Ellensburg, *Brandegee 636* (UC); **Okanogan Co.:** near Tonasket, *Thompson 7106* (DS,GH,MO,OSC,UC,US,WTU); **Yakima Co.:** Squaw Creek, *Cotton 874* (GH, MO, US,WS). **Wyoming. Albany Co.:** S. of Laramie, *Beetle 4894* (COLO,GH,OSC,PH,POM,TEX, UC,WIS); **Fremont Co.:** Red Canyon of the Wind River, 13 miles S. of Dubois, *C. & M. Porter 7503* (DS,NY,RM,RSA,UC); **Goshen Co.:** S. of Torrington, *Osterhout 7564* (RM); **Laramie Co.:** near Cheyenne, *Seal s.n.*, 1877 (PH); **Lincoln Co.:** 5.3 miles W. of Fossil bed marker on U.S. Hwy. 30N, ca. 18 miles W. of Kemmerer, *I. & M. Al-Shehbaz 6977* (GH); **Niobrara Co.:** Lusk, *Nelson 574* (GH,MO,NY,PH,RM,UC,US); **Sheridan Co.:** Dayton, *Tweedy 2419* (NY); **Sweetwater Co.:** Granger, Hams Fork, *Nelson 4140* (RM); **Uinta Co.:** Blacks Fork River, 4 miles N.W. of Lyman, *Rollins & Muñoz 2922* (DS,GH,RM,UC,UTC); Yellowstone National Park: Mammoth Hot Springs, *I. & M. Al-Shehbaz 68161* (GH).

Thelypodium integrifolium subsp. *integrifolium* as defined here shows a rather wide range of variation in a number of characters. Despite the fact that some of the variation, as is shown below, falls in certain geographic patterns, the present writer believes that the taxonomy of the group is better served by maintaining subsp. *integrifolium* as a polymorphic taxon rather than splitting it into five or six varieties.

Nectar glands are more variable here than in the other four subspecies of *Thelypodium integrifolium* (Plate 7). They tend to be low and flat in most plants of central and northern Colorado, Wyoming, and central and northern Utah. On the other hand, plants of North Dakota and South Dakota have somewhat bilobed glands, while those of Oregon, Washington, and some parts of Idaho have well-developed glands that are toothlike and up to 1 mm. high. However, the variation is of a continuous nature and does not seem to characterize all the populations of any given part of the geographic range. Moreover, plants of the same population may vary considerably in the size, shape, and height of their nectar glands.

The fruiting pedicels are equally variable. Although most of the populations of subsp. *integrifolium* are characterized by having slender pedicels that are somewhat flattened at the base, populations of central and northern Colorado, southwestern Wyoming, and northern Utah tend to have stouter pedicels that are hardly flattened at the base. The length of the pedicel is also subject to considerable variation. The shortest pedicels are found in the populations of southwestern Wyoming and northern Utah, while the longest pedicels are characteristic of the plants from Washington, North Dakota, and South Dakota.

Flower color ranges from lavender to various shades of purple, or

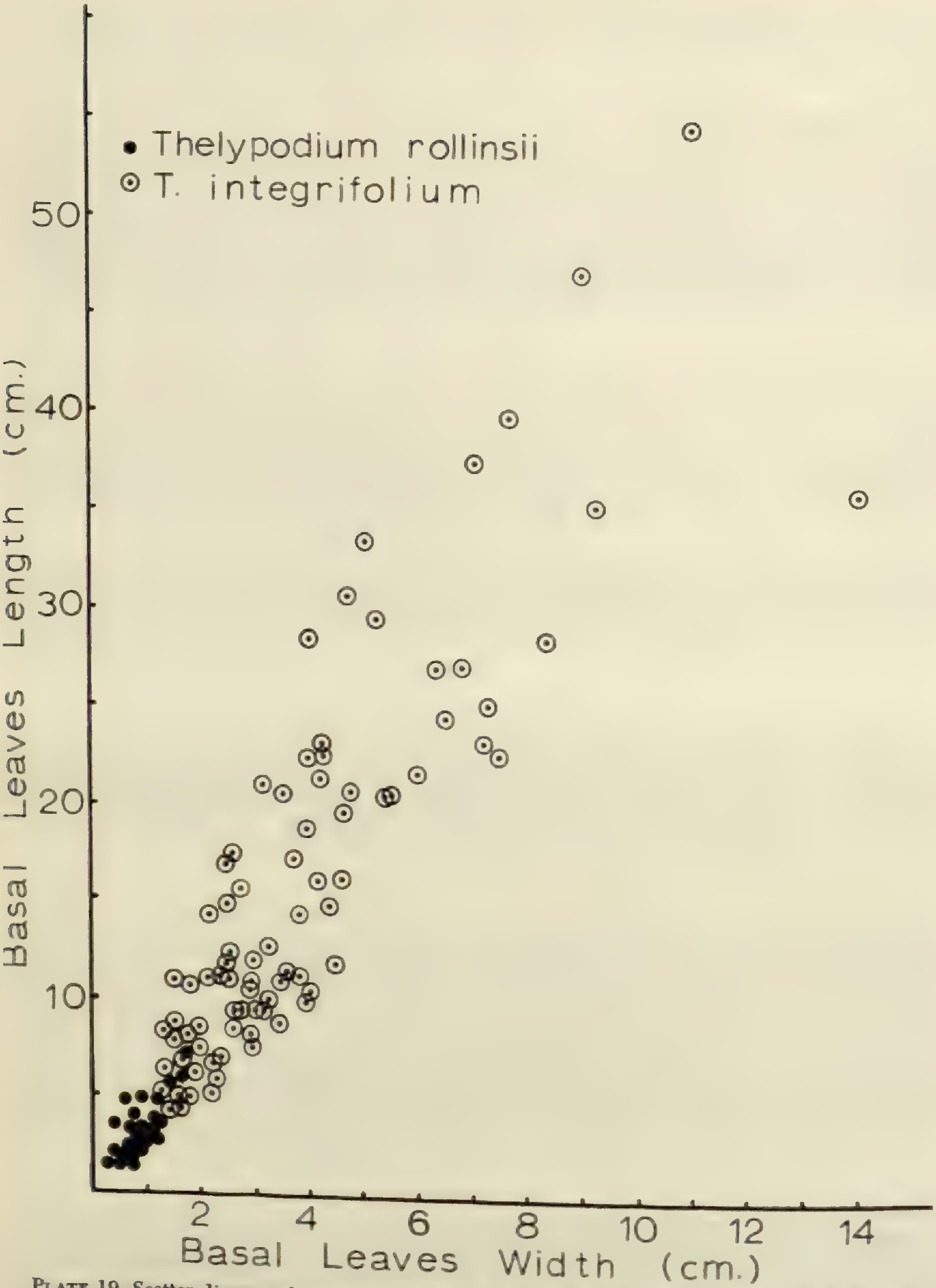


PLATE 19. Scatter diagram showing relationship of length to width of basal leaves of *Thelypodium integrifolium* and *T. rollinsii*.

sometimes white. In central Colorado the populations of this subspecies tend to have dark purple flowers, while those of North Dakota and South Dakota are made up of white-flowered forms. Flower color may be variable in the same population. The present writer has collected plants from populations in northwestern Wyoming and central Idaho that are nearly white, lavender, or purple-flowered growing but a few yards apart.

Finally, the infructescences tend to be shorter in the populations of western Wyoming, northern Utah, Montana, and adjacent Idaho than in other parts of the subspecies range. However, forms with short infructescences are by no means restricted to the populations of the states mentioned. In fact, they are distributed throughout the subspecies range but with much less frequency in areas outside of that indicated. Plants of this nature were the basis of Payson's *Thelypodium lilacinum* var. *subumbellatum*. The type collection of this variety has been compared carefully with an isotype of *T. integrifolium* at the Gray Herbarium. There are no significant differences between the two and nothing to justify the recognition of the former taxon.

The three features claimed by Greene (1901) to distinguish *Thelypodium lilacinum* from *T. integrifolium* (corymbose inflorescence that lengthens in fruit, rich lilac-purple flowers, and branching from the base) are clearly variable within the type collection of *T. lilacinum*. Moreover, the characters used by Payson (1923) to distinguish the two have no claim to consistency. *Thelypodium lilacinum* may deserve a rank no higher than variety at best, but if this course is followed, then subsp. *integrifolium* should be further split into a number of varieties separated from each other by only a few inconsistent characters. This would certainly confuse rather than clarify the taxonomy of the complex.

Subspecies *integrifolium* is the most widely distributed of the five subspecies of *T. integrifolium*. It has been reported from Owyhee County in Idaho (Baker 1963), and Dawes Co., Deuel Co., Box Butte Co., Sheridan Co., (Peterson 1912, 1923) and Garden Co. (Winter 1936) in Nebraska. I have not seen specimens from any of these counties, but there is no reason to doubt the occurrence of it there.

7b. **Thelypodium integrifolium** (Nuttall) Endlicher subsp. **complanatum** Al-Shehbaz subsp. nov.

Petalis lilacinis vel albis, (5)6–8.5(9.5) mm. longis; infructescentibus racemosis congestis, (0.6)1.2–7(9) cm. longis; pedicellis fructiferis horizontalibus vel divaricatis, striatis, rectis, crassis vel tenuibus, ad basin valde complanatis, 3–5(6) mm. longis; siliquis stipitatis, divaricatis vel divaricato-adscendentibus, (0.9)1.4–2.7(3.4) cm. longis; stipite crasso, 0.5–1(3) mm. longo.

Holotype in the Gray Herbarium, collected on low alkaline ground, 10 miles east of Ironside on U.S. Hwy. 26, about ¼ mile south of the highway, Malheur County, Oregon, August 16, 1969, *Ihsan & Mona Al-Shehbaz 6956;* isotypes to be distributed.

Flowers mostly lavender, or rarely white; petals (5)6–8.5(9.5) mm. long; infructescence a short raceme, strongly congested, central rachis (0.6)1.2–7(9) cm. long; mature fruiting pedicels mostly stout, or rarely slender, straight, striate, mostly horizontal, or sometimes divaricate, strongly flattened at base, 3–5(6) mm. long; siliques straight or curved, divaricate to divaricately ascending or horizontal, (0.9)1.4–2.7(3.4) cm. long; gynophores stout, 0.5–1(3) mm. long; nectar glands low, flat to more often bilobed, with the lobes partly united to free.

Flowering mainly from late June through August at elevations from 2,900 to 8,000 feet in eastern California, Nevada, southeastern Oregon, and northwestern Utah (Map 3).

PLATE 20. Infructescences (main branches) of *Thelypodium integrifolium* subsp. *complanatum* (FIG. 1) and *T. rollinsii* (FIG. 2). Scale: one centimeter.

REPRESENTATIVE SPECIMENS. **California. Inyo Co.:** Black Canyon, White Mountains, *Duran* 532 (CAS,DS,F,GH,LA,MICH,MO,NY,ORE,POM,RM,UC,US,UTC,WIS); **Lassen Co.:** Rush Creek, 17.5 miles E. of U.S. Hwy. 395 and 1.3 miles W. of Nevada state line, *Bacigalupi & Robbins* 5428 (JEPS); **Mono Co.:** Sherwin Grade summit, *Kerr s.n.*, 1936

(CAS,GH,US). **Nevada. Elko Co.:** 2.7 miles S. of Jackpot on U.S. Hwy. 93, *I. & M. Al-Shehbaz 6926* (GH); 13.8 miles N.E. of Elko on Interstate Hwy. 80, *I. & M. Al-Shehbaz 6934* (GH); vicinity of Nevada Industrial School, U.S. Hwy. 40, *Maguire & Holmgren 22169* (DS,GH,NA,NY,UC,US,UTC,WS,WTU); **Humboldt Co.:** Virgin Creek gorge, Sheldon Range, *Murie 2752* (NA); **Lander Co.:** 3–18 miles N. of Austin along Hwy. 8A, *Goodner & Henning 874* (NA,NY); **Lyon Co.:** 6½ miles S.E. of Rockland, *Hendrix 655* (UC); **Mineral Co.:** 1 mile S. of Fletcher, *Alexander & Kellogg 4487* (DS,GH,UC,US,UTC); 1.3 miles from mouth and up Cory Creek, Wassuk Range, *Archer 6874* (NA,NY,RSA,TEX,UC,UTC,WTU); **Nye Co.:** 23 miles S. of Dieringer, *Goodner & Henning 728* (NA,NY); vicinity of Millet, *Goodner & Henning 1162* (DS,F,MO,NA); **Washoe Co.:** Truckee Pass, *Heller 9958* (DS,F,GH,MO,NY,PH,US); Wadsworth, *Palmer 22* (F,MO,NA,NY,UC); **White Pine Co.:** Snake Range, Miller Basin Wash, T. 15 N., R. 68 E., Sec. 19, *Holmgren & Reveal 1640* (GH,MICH,NY,RSA,TEX,UC,UTC,WS,WTU). **Oregon. Harney Co.:** 6.3 miles E. of Burns on Oregon Hwy. 78, then 0.9 miles S. of the highway on a dirt road, *I. & M. Al-Shehbaz 68141* (GH). **Utah. Box Elder Co.:** north end of Salt Lake, *Anderson 855* (UTC); 18 miles W. of Park Valley, *Maguire & Holmgren 22241* (DS,GH,NY,UTC,WTU).

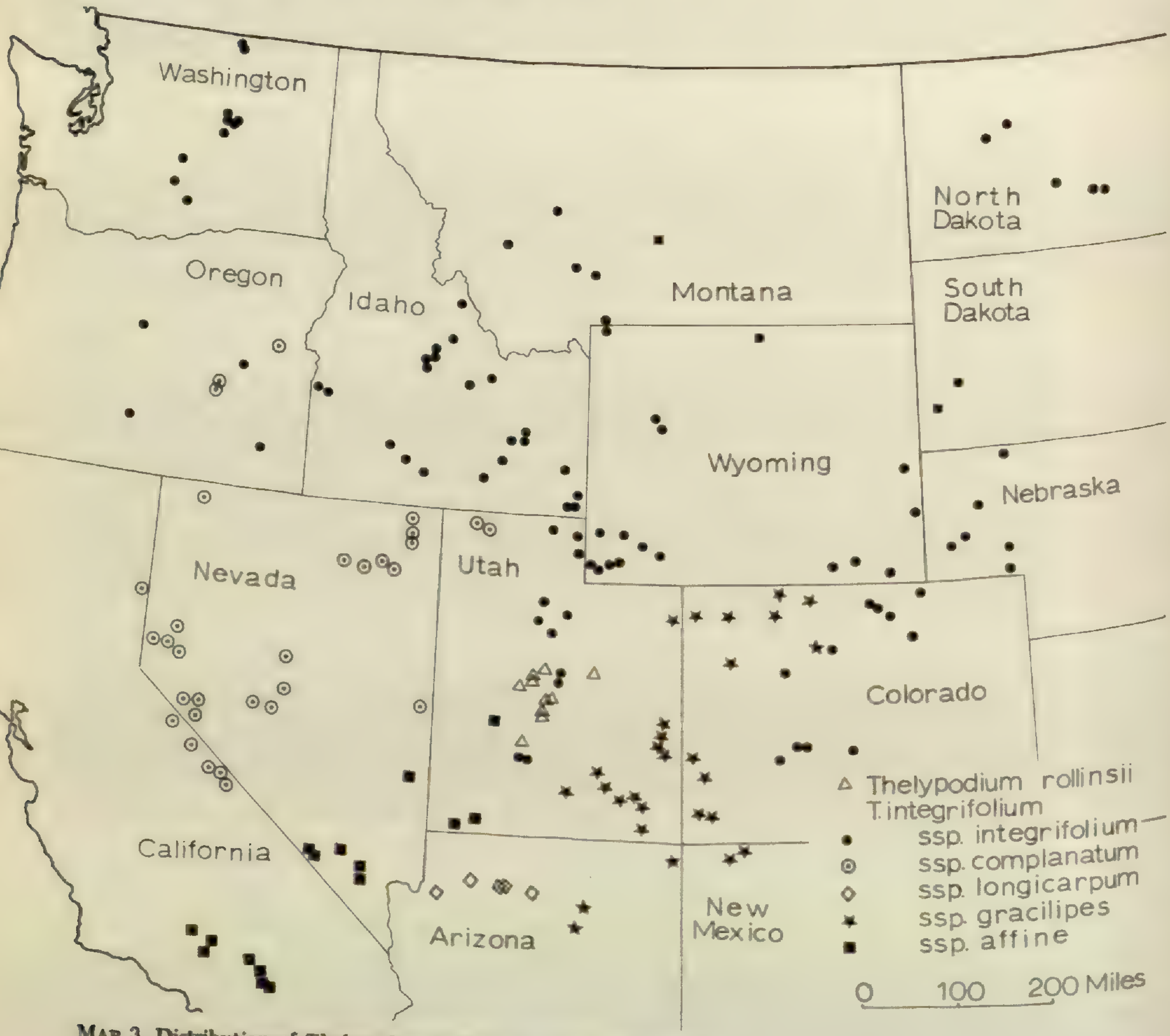
Thelypodium integrifolium subsp. *complanatum* corresponds fairly well with *T. rhomboideum sensu* Payson (1923). However, the type specimen of *T. rhomboideum* Greene, which Payson did not see (Payson, 1923, p. 276), differs in many significant morphological features from the specimens cited by him under this "species." In fact, the type specimen of *T. rhomboideum* is hardly different from that of *T. affine* Greene. The type of *T. rhomboideum* was collected from the West Humboldt Mountains by Greene. These mountains are located, according to McVaugh and Fosberg (1941), in Pershing County (Nevada), and are now known as the Humboldt Range. The mature fruiting pedicels of the type of *T. rhomboideum* are 7–8 mm. long. This clearly falls within the range of subsp. *affine* and not subsp. *complanatum*. The fruiting pedicel length of plants of *T. integrifolium* from central Nevada, placed here in subsp. *complanatum*, hardly exceed 5 mm. in length. The nectar glands on the type of *T. rhomboideum* are very well-developed and approximately 1 mm. in length. This is characteristic of most plants of subsp. *affine* and not subsp. *complanatum*. The only clear difference between the type collection of *T. affine* and *T. rhomboideum* is the shape of the basal leaves, which is spatulate-oblanceolate in the former and rhombic-lanceolate (broadly elliptic-lanceolate) in the latter. The type collection of the latter "species" is made up of a rosette and a flowering specimen each mounted on a separate sheet. Our experience with basal leaf shape in *T. integrifolium* and other species leads us to the conclusion that this is one of the most variable and least satisfactory taxonomic characters to use in distinguishing taxa at all levels in *Thelypodium*.

All the evidence at hand supports the following conclusions: (1) the type of *Thelypodium rhomboideum* is nothing but a minor variant of *T. affine;* (2) subspecies *complanatum* is the sole representative of *T. integrifolium* in central and northern Nevada; and (3) it is probable that the type specimen of *T. rhomboideum* was collected from an area very near to the known range of subsp. *affine*.

7c. **Thelypodium integrifolium** (Nuttall) Endlicher subsp. **gracilipes** (Robinson) Al-Shehbaz, comb. nov.

Thelypodium integrifolium (Nutt.) Endl. var. *gracilipes* Robins. in Gray, Syn. Fl. N. Am. 1:176. 1895. Holotype: southwestern Colorado, *T. S. Brandegee 1233* (GH).
Thelypodium gracilipes (Robins.) Rydb., Fl. Colo. 167. 1906.
Pleurophragma gracilipes (Robins.) Rydb., Bull. Torr. Bot. Club 34:433. 1907.
Thelypodium rhomboideum Greene var. *gracilipes* (Robins.) Pays., Ann. Mo. Bot. Gard. 9:277. 1923.
Pleurophragma platypodum Rydb., Bull. Torr. Bot. Club 34:434. 1907. Holotype: Moab, Grand County, Utah, August 30, 1891, *Marcus E. Jones s.n.* (NY); isotypes: CAS,DS,GH,MICH,MO,NY,POM,RM,TEX,UC,US,WS.

Flowers white to lavender, rarely purple; petals (5)6.5–9(10) mm. long; infructescence a long raceme, moderately congested, central rachis (3)8–20(28) cm. long; mature fruiting pedicels mostly stout, or rarely slender, straight, sometimes slightly striate, horizontal, less often divaricate or slightly reflexed, strongly flattened at base, (2)2.5–4.5(6) mm. long; siliques straight to more often curved, horizontal to divaricate or slightly reflexed (0.8)1.5–2.5(3.3) cm. long; gynophore slender to rarely stoutish, (0.5)0.75–3(4) mm. long; nectar glands low and flat, or more often bilobed, with the lobes partly to completely fused.



Map 3. Distribution of *Thelypodium rollinsii* and *T. integrifolium*.

Flowering July through August at elevations between 3,500 to 8,300 feet in northwestern New Mexico, northeastern Arizona, western Colorado, and eastern Utah. (Map 3).

REPRESENTATIVE SPECIMENS. **Arizona. Apache Co.:** Navajo Indian Reservation, N. end of Carrizo Mts., *Standley 7412* (US); **Coconino Co.:** Painted Desert, near Tuba, *Clute 82* (GH,MO,NY,RM,US). **Colorado. Grand Co.:** Middle Park, near Hot Sulphur Springs, *Ramaley & Robbins 3627* (COLO,RM); **Jackson Co.:** Lake John, *Johnson 907* (COLO); **Moffat Co.:** S. bank of Yampa River, 1 mile W. of Maybell, *Hermann 5352* (GH,PH); **Montrose Co.:** Bedrock, *Walker 369* (GH,RM,US,WS); **Montezuma Co.:** 5 miles N.W. of Cortez on U.S. Hwy. 160, *I. & M. Al-Shehbaz 6994* (GH); **Rio Blanco Co.:** Rio Blanco, *Robbins 7060* (COLO); **Routt Co.:** Hayden, *Goodding 1789* (COLO,GH, MO,NY,RM,UC); **San Miguel Co.:** along Dolores River at the bridge on Colorado Hwy. 80, *Ownbey 1494* (COLO,GH,MO,NY,RM,UC,WS,WTU). **New Mexico. San Juan Co.:** Farmington, *Wooton 2783* (NMC,US); vicinity of Cedar Hill, *Standley 7992* (US). **Utah. Garfield Co.:** 15.1 miles E. of Escalante, Utah Hwy. 54, Calf Creek Recreation Area, *N. & P. Holmgren 4721* (GH); **Grand Co.:** Hanging Garden, N. of trail to Delicate Arch, Arches National Monument, *Welsh, Harrison & Moore 2337* (NY); **San Juan Co.:** Natural Bridges National Monument, *I. & M. Al-Shehbaz 6993* (GH); Lime Creek, 5 miles N. of Mexican Hat, *Cutler 2781* (DS,GH,NA,NY); **Uintah Co.:** S. of Split Mt. Gorge, Dinosaur National Monument, *Bradley 5338* (COLO).

Thelypodium integrifolium subsp. *gracilipes* is probably the best defined of all the five subspecies. Occasionally it has been confused with the plants cited here under subsp. *complanatum*. Payson (1923), for instance, treated it as a variety of *T. rhomboideum*, but confused the two by citing some of the collections that unquestionably belong to subsp. *gracilipes* under *T. rhomboideum* proper. This was probably the result of his use of the gynophore length as the basis of distinguishing the two taxa. Rydberg (1923), on the other hand, recognized two species, namely *Pleurophragma gracilipes* and *P. platypodum*. He claimed that the two are distinguishable on the basis of having pedicels that are not flattened and about 1 cm. long in the former "species," while they are flattened at the base and about 3 mm. long in the latter. These alleged differences have no claim to reality. The type collections of the two taxa are very similar, and the pedicels in both are flattened and less than 5 mm. long. Moreover, Rydberg's own annotations show that he had designated the isotypes of his *P. platypodum* differently. For example, two isotypes at NY were annotated as *Thelypodium platypodum*, one at NY and one at US as *T. integrifolium*, and the GH isotype as *T. integrifolium* var. *gracilipes*.

Subspecies *gracilipes* is rather variable as far as flower color is concerned. The populations of northern Colorado tend to have mostly lavender to dark purple flowers, while those of eastern Utah and southwestern Colorado often have lavender as well as white-flowered forms within the same population. The populations of Arizona and New Mexico appear to be exclusively white flowered. The infructescence length also is somewhat variable. Populations of northern Colorado and adjacent northeastern Utah tend to have shorter infructescences than those else-

where in the subspecies range, but the variation is of a continuous nature.

Subspecies *gracilipes* is most closely related to subsp. *complanatum* from which it is distinguished by its longer infructescence and longer and more slender gynophores. The two subspecies can be distinguished from the other three of *T. integrifolium* by their shorter pedicels that are often strongly flattened at the base.

7d. **Thelypodium integrifolium** (Nuttall) Endlicher subsp. **affine** (Greene) Al-Shehbaz, comb. nov.

Thelypodium affine Greene, Pittonia 4:314. 1901. Holotype: Tehachapi, Kern County, California, June 22, 1889, *E. L. Greene s.n.* (ND–G).

Thelypodium rhomboideum Greene, Pittonia 4:314. 1901. Holotype: West Humboldt Mountains, July 1894, *E. L. Greene s.n.* (ND–G).

Pleurophragma rhomboideum (Greene) O. E. Schulz, Bot. Jahrb. 66:98. 1933.

Sepals whitish-green; petals white, (5)6–9(10) mm. long; infructescence racemose, often congested, central rachis (3.7)4.5–12(16.5) cm. long; fruiting pedicels straight, sometimes slightly curved, strongly to moderately striate, mostly horizontal, sometimes divaricate or slightly reflexed, mostly whitish to whitish-green, often moderately flattened at base, stout to rarely slender, (5)6–9(13) mm. long; siliques often curved upwards, horizontal to divaricate, rarely divaricately ascending, (1.4)1.9–3.7(4.5) cm. long; gynophores stout, (0.5)1–3 mm. long; nectar glands large, up to 1 mm. high, well-developed above the base of single stamens, lobed, with the lobes partly to completely fused, or sometimes free, often strongly flattened and erect in the middle.

Flowering late June to mid October, but mainly late July through September, at elevations from 2,000 to 5,800 feet in southeastern California, southern and southeastern Nevada, and southwestern Utah (Map 3).

REPRESENTATIVE SPECIMENS. **California. Kern Co.:** Tehachapi, *Eastwood s.n.*, 1894 (GH); **Los Angeles Co.:** Rosamond Lake, *Eastwood & Howell* 3979 (CAS); Lancaster, *Jones s.n.*, 1924 (POM,UC); **San Bernardino Co.:** El Vaquero Rancho, ca. 29 miles S.E. of Victorville on California Hwy. 18, *I. & M. Al-Shehbaz 68128* (GH); Rabbit Springs near Lucerne Valley, *Ball 14391* (CAS,COLO,NA,RM,RSA); 1 mile N.W. of Cushenbury Springs, *Munz 12766* (DS,F,MO,POM,UC). **Nevada. Clark Co.:** ca. 8 miles N.W. of Henderson on U.S. Hwy. 95, *I. & M. Al-Shehbaz 6988* (GH); Cactus Springs, Indian Springs Valley, *Beatley 9510* (GH); **Lincoln Co.:** 4 miles S. of Caliente, below road to Ryan State Park, *Train 2450* (NA,NY,UC); **Nye Co.:** 0.5 miles E. of Carson Slough on road to Spring Meadows Farm, Sec. 5, T. 18 S., R. 50 E., *Reveal 1537* (GH). **Utah. Kane Co.:** 4–5 miles S.W. of Mollie's Nipple and 40–45 miles N.E. of Kanab, *Hester 1052* (NA); **Millard Co.:** Pumice, near Black Rock, *Jones s.n.*, 1913 (POM); **Washinton Co.:** 0.2 miles E. of Rockville on Utah Hwy. 15, *I. & M. Al-Shehbaz 6987* (GH); vicinity of St. George, *Maguire & Richards 20460* (DS,UTC).

Subspecies *affine* and *longicarpum* are the least variable of the five subspecies of *T. integrifolium*. The tallest plants in *Thelypodium* are found in these two subspecies, but short plants are found here as well. The only two characters that are variable to a significant extent are the pedicel and fruit length, but these two characters are equally or more variable in the other three subspecies.

Subspecies *affine* was known only from southeastern California for a

long time. It was first reported from Utah by Maguire (1942) as *Thelypodium affine*, and the range as presently given extends to cover southern and southeastern Nevada.

The closest relative to subsp. *affine* is subsp. *longicarpum* from which it is distinguished by its shorter siliques and petals. The two are easily distinguished from the remaining three subspecies of *Thelypodium integrifolium* on the basis of their white flowers, whitish-green sepals, and fruiting pedicels that are stout, whitish-green, and longer than in the others.

7e. **Thelypodium integrifolium** (Nuttall) Endlicher subsp. **longicarpum** Al-Shehbaz, subsp. nov.

Sepalis albis vel viridi-albis; petalis albis, (7.5)8–11(13) mm. longis; infructescentibus racemosis, congestis (4.3)8–20 cm. longis; pedicelis fructiferis crassis, rectis, moderate vel valde striatis, albidis, ad basin valde complanatis, saepe horizontalibus vel reflexis, rarissime divaricatis, (6)7–11(13) mm. longis; siliquis stipitatis, torulosis, rectis vel arcuatis vel incurvatis, horizontalibus vel reflexis, (2.2)3.5–6.3(8.0) cm. longis; stipite crasso, (1)1.5–4(5.5) mm. longo.

Holotype in the Gray Herbarium, collected ca. 0.5 mile below Indian Garden on Bright Angel Trail, Grand Canyon National Park, Coconino County, Arizona, September 13, 1969, *Ihsan & Mona Al-Shehbaz 6991;* isotypes to be distributed.

Sepals creamy white to white below and greenish above; petals white, very rarely lavender, (7.5)8–11(13) mm. long; infructescence racemose, moderately to strongly congested, central rachis (4.3)8–20 cm. long; fruiting pedicels straight, stout, moderately to strongly striate, whitish, often strongly flattened at base, mostly horizontal to reflexed, rarely divaricate, (6)7–11(13) mm. long; siliques often strongly torulose, straight to incurved, sometimes arcuate, horizontal to reflexed, rarely divaricate or divaricately ascending, (2.2)3.5–6.3(8.0) cm. long; gynophore stout, (1)1.5–4(5.5) mm. long; nectar glands up to 1 mm. long, each with two well-developed tooth-like processes that are partly to completely free.

Flowering early August through October at elevations from 1,900 to 4,200 feet in the Grand Canyon National Park and the adjacent areas in northern Arizona.

REPRESENTATIVE SPECIMENS. **Arizona. Coconino Co.:** Havasu Falls, Havasupai Canyon, *Clover 4408* (DS,MICH); below Mooney Falls, *Clover 5263* (DS); village in Havasupai Canyon, *Clover 7016* (MICH,US); Shuiamo Creek, *Pilshy s.n.*, 1906 (PH); Indian Spring, Bright Angel Trail, *Seler 4744* (CAS,GH,US); Bright Angel Trail at Colorado River, *Wolf 3180* (CAS,DS,GH,RSA); **Mohave Co.:** between Quartermaster Canyon and Upper Travertine Falls, Lake Mead, *Clover 4284* (DS); Saddle Horse Springs, Grand Canyon National Monument, Toroweap, *Cottam 13526* (UT); Outer Gorge, Grand Canyon National Monument, Toroweap, *Cottam 13837* (CAS,US,UT); Quartermaster Canyon, W. end of Grand Canyon, *Grater 210* (UC).

Subspecies *longicarpum* has been confused with other taxa of the *Thelypodium integrifolium* complex. It was cited as *T. integrifolium* by Clover and Jotter (1945) and Kearney and Peebles (1960), and as *T. rhomboideum* by the first two authors and by Kearney and Peebles (1942). The latter authors failed to distinguish it from the very distinct subsp. *gracilipes*, as judged from their citation of collections belonging to the two subspecies.

The long siliques and pedicels of subsp. *longicarpum* serve to distinguish it easily from the other subspecies of *Thelypodium integrifolium*. One might argue that these features are different enough from the rest of *T. integrifolium* for it to be recognized as a distinct species. However, these features are connected with the rest of *T. integrifolium* through subsp. *affine*. Furthermore, the similarities in the flower and leaf morphology as well as the mustard oils (Table 6) in the whole complex are evidence against the recognition of subsp. *longicarpum* as a distinct species.

Thelypodium integrifolium is clearly the most variable and most widely distributed of any species of the genus. It occupies an extremely wide range of habitats. It grows on clay, loamy or sandy soils that are slightly to strongly alkaline, on open flats or meadows, shady areas under shrubs, dry deserts, and along wet streamsides. It is also common on mineralized soils near hot springs. None of the subspecies is restricted to one particular type of habitat, although subsp. *gracilipes* and *longicarpum* appear to favor sandy soils.

Plants of the southern and western portions of the species range tend to be taller than those of the northern and eastern parts. However, there are a few exceptions. The tallest plants are found in subsp. *longicarpum* and *affine*, while the shortest are found in subsp. *integrifolium* particularly in the populations of northern Utah, Colorado, and Wyoming. In these populations some of the plants do not exceed one foot, while those of subsp. *affine* may exceed nine feet in height.

Thelypodium integrifolium is a complex species. It is made up of a large series of populations that fall into morphologically distinct groups, which are geographically defined, and seem to represent natural infraspecific taxa. Some botanists, namely Payson (1923), recognized four species and two varieties in this complex. The characters he used in distinguishing these "species" (nectar glands and gynophore length) are probably the most variable and inconsistent in this complex. Abrams (1944), on the other hand, took the position that a single polymorphic species is represented, and he did not recognize any infraspecific taxa.

The present writer believes that the taxonomy of this complex can be best served by recognizing these natural groups as subspecies instead of species. There seems to be a certain amount of interdigitation between these subspecies. This is true between subsp. *complanatum* and subsp. *integrifolium* in central Oregon, and between the latter subspecies and *gracilipes* in northern Colorado. However, it is clear that experimentation and further field work are needed before more can be profitably said about this. Each of the five subspecies can be determined rather easily, if the characteristics of the pedicels and the siliques are carefully studied and the geographic range is taken into account. However, there is a clear overlap between the five subspecies of *Thelypodium integrifolium* in the lengths of their fruiting pedicels and siliques (Plate 21).

Thelypodium integrifolium can be easily distinguished from other species of the genus on the basis of its cauline leaves that are nearly always without auricles and by the nectar glands that are usually elevated and tooth-like, but present only around the lateral stamens.

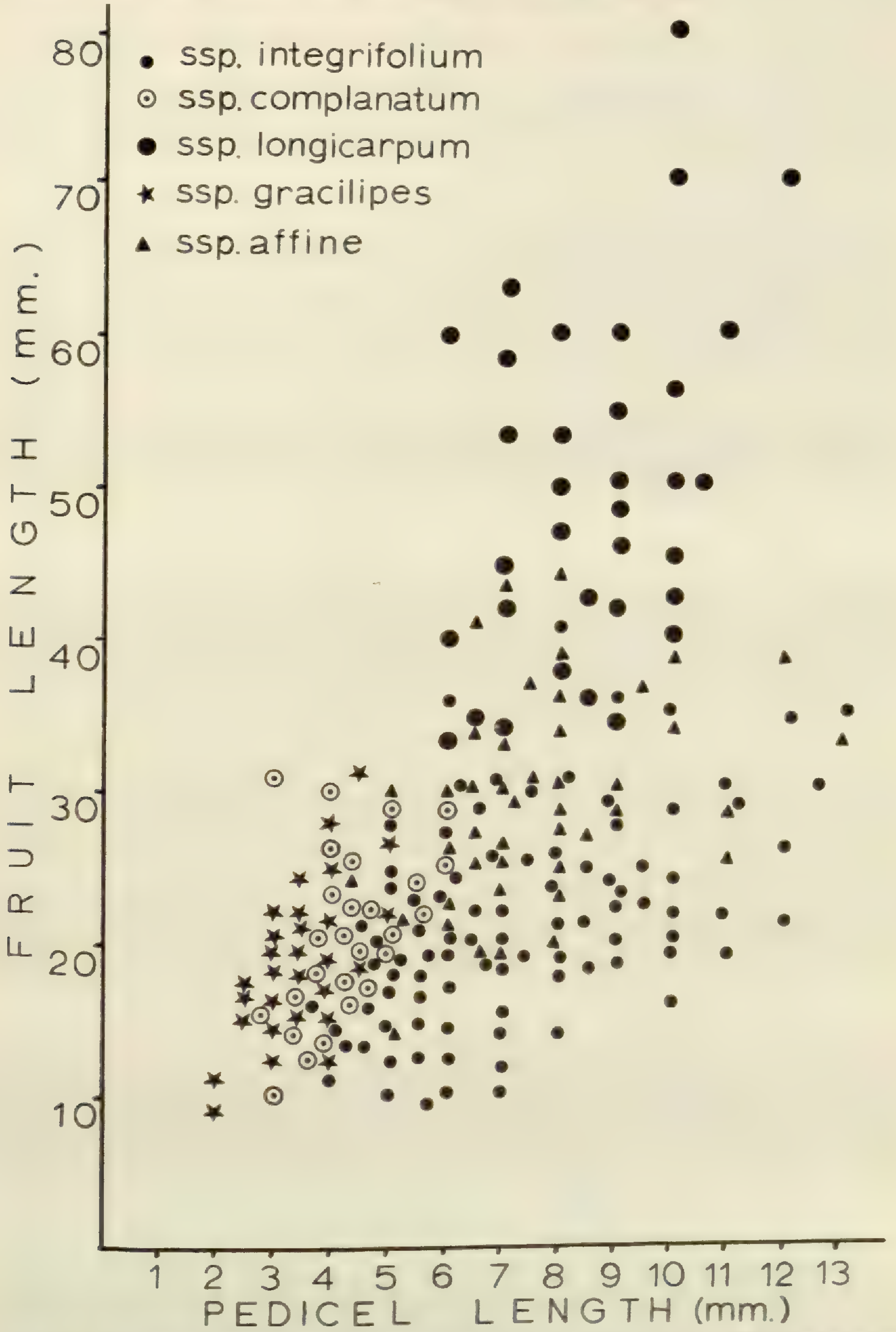


PLATE 21. Scatter diagram showing relationship of fruiting pedicel length to silique length in the five subspecies of *Thelypodium integrifolium*.

8. **Thelypodium stenopetalum** Watson

Thelypodium stenopetalum Wats., Proc. Amer. Acad. 22:468. 1887. Holotype: stony hillside, Upper Lake (now known as Baldwin Lake), Bear Valley, San Bernardino Mountains, San Bernardino County, California, June 1886, *Samuel B. Parish 1794* (GH); isotype: DS.

Thelypodiopsis stenopetala (Wats.) O. E. Schulz, Bot. Jahrb. 66:99. 1933.

Plants biennial, glabrous and glaucous throughout; stems mostly branched from the base, decumbent to subdecumbent, sometimes simple or branched above, (2.6)3.1–8(9) dm. high; basal leaves thickish, oblong to oblanceolate, sometimes ovate to spatulate, obtuse to rarely acute, entire, or sometimes repand at margin, 3.8–15(18) cm. long, 1.5–3.4(4.2) cm. wide; petioles glaucous, ciliate near the base, 1–4.5(6) cm. long; cauline leaves glabrous and glaucous, ascending, sagittate to amplexicaul at the base, rarely auriculate, mostly lanceolate to oblong-lanceolate or oblong, rarely linear to lanceolate-linear, entire, obtuse, or acute at apex, (1.3)1.6–4.8(6.1) cm. long, (0.3)0.5–0.9(1.5) cm. wide; basal lobes acute to obtuse, deltoid to oblong, (1)2–8(10) mm. long, 1–3 (4) mm. wide; inflorescence a long raceme, almost always lax; floral buds oblong-linear; sepals erect, non-saccate, linear to oblong-linear, obtuse, scarious at margin, purple above and green below or purple-green throughout, (6)6.5–9(10) mm. long, 1–1.5(1.75) mm. wide; petals linear to narrowly linear, crisped mainly between claws and blades, (8)9.5–15(16.5) mm. long, 0.3–0.5(0.75) mm. wide, blades horizontal, mostly lavender, or rarely white; claws erect, 4–6.5 (8.5) mm. long; filaments erect, white to somewhat lavender, slightly dilated at base, somewhat tetradynamous, single filaments (5.5)7–11(12) mm. long, paired filaments (7)8–12.5(14) mm. long; anthers exserted, sagittate at base, linear to narrowly oblong, coiled when fully dehisced, often purplish, 3.5–5(6) mm. long; glandular tissue low and flat, well-developed and surrounding base of single filaments, narrower and subtending base of paired filaments; fruiting pedicels stout, not flattened at base, ascending to divaricately ascending, rarely divaricate to horizontal, straight or rarely curved, (3.5)4–8 mm. long; siliques straight or slightly incurved, terete to rarely more or less quadrangular, slightly torulose, usually stout, ascending to divaricately ascending, rarely divaricate (2.2)2.8–4.9(6.3) cm. long, 1–1.5(1.75) mm. wide; styles slender, terete, 1–2(2.5) mm. long; stigmas entire; gynophores stout, 0.5–3.5(5) mm. long; seeds 1–1.3(1.5) mm. long, 0.75 mm. wide; cotyledons obliquely incumbent, or rarely incumbent.

Flowering late May to early August at elevations from 6,500 to 6,800 feet in the Bear Valley of California.

REPRESENTATIVE SPECIMENS. **California. San Bernardino Co.:** 2.2 miles E. of Big Bear City from junctions of California Hwys. 18 and 38, southern shore of Baldwin Lake, *I. & M. Al-Shehbaz 6947* (GH); E. end of Bear Lake, *Munz 10463* (POM); N. shore of Baldwin Lake, *Peirson 6741* (RSA); Bear Valley, *Parish 3787* (F,GH,JEPS,ND–G, US); near Big Bear Post Office, *Yates 6634* (UC).

Thelypodium stenopetalum is one of the most retricted species of the genus. It appears to be endemic to alkaline soils of the shores of Baldwin Lake and the nearby areas of Bear Valley. It was said to grow on stony hillsides by Robinson (1895), Payson (1923), Jepson (1936), and Munz (1959). However, these authors apparently depended on the original description of the species, which cites such a habitat, as there are no other collections, to my knowledge, carrying that information. The present writer failed to find this species on the stony hillsides of Bear Valley in 1968.

Thelypodium stenopetalum is rather unique in the genus in having narrowly linear petals, which distinguish it easily from the other species of *Thelypodium*. It can be distinguished also from the other auriculate-leaved species by a combination of the following characters: stout and usually ascending pedicels, oblong-linear to linear floral buds, and racemose inflorescences that are long and lax.

9. **Thelypodium howellii** Watson

Herbaceous biennial; stems mostly single from the base, usually branched above, sparsely to densely hirsute or hirsute-hispid near the base, glabrous and somewhat glaucous above or throughout, 1–8(9.3) dm. high; basal leaves oblanceolate to spatulate, less often oblong to lanceolate, lyrately lobed to dentate, sometimes entire or repand, obtuse or sometimes acute at apex, sparsely pubescent to more often glabrous, usually glaucous, 2–10(13.5) cm. long, 1–2.3(4) cm. wide; petioles slender, 0.5–2 cm. long, ciliate near or at the base; cauline leaves lanceolate to linear-lanceolate, sometimes linear to oblong, acute to acuminate at apex, entire, often strongly sagittate to amplexicaul at base, rarely auriculate, glabrous and glaucous, (0.8)1–9.7(14.5) cm. long, 0.2–1(3) cm. wide; basal lobes lanceolate to oblong or ovate, acute to obtuse, 0.1–1.5(2.3) cm. long, (0.5)1–6(11) mm. wide; inflorescence raceme, lax; sepals erect, scarious at margin, green in the center and lavender or purple at margin, or lavender throughout, (3.5)5–8.5(11.5) mm. long, median sepals linear to lanceolate-linear, often somewhat hooded near the apex, with the subapical appendages small or up to 1.3 mm. long, sometimes slightly saccate at base, (0.75)1–1.5(2) mm. wide, lateral sepals often lanceolate, usually saccate at base, 1.5–2(2.5) mm. wide; petals linear or oblanceolate to spatulate, partly to completely crisped, lavender to purple, (6)9–16.5(22) mm. long, (0.5)0.75–2.7(3) mm. wide; claws erect, (2.5)4–7(11) mm. long; filaments erect, white to lavender or purple, somewhat tetradynamous, single filaments curved at the base, (2.5)4.5–8(10) mm. long, paired filaments erect, partly to completely fused or free, (3)5.5–9(12) mm. long; anthers purple, somewhat exserted to nearly included, sagittate at base, linear-lanceolate to linear, (1.5)2–4(5.5) mm. long; glandular tissue flat, well-developed and surrounding base of single stamens, less developed and subtending base of paired stamens; fruiting pedicels stout, mostly ascending, rarely divaricately ascending, straight to sometimes slightly curved, not flattened at base, (2.5)3.5–8(14.5) mm. long; siliques terete, straight to sometimes slightly incurved, mostly ascending, or sometimes nearly erect to divaricately ascending, torulose, mostly forming a straight line with pedicels, (1.5)2–6.2(8.2) cm. long, 1–1.25(2) mm. wide; gynophores 0.5–1(3.5) mm. long; styles slender to somewhat stout, cylindrical to nearly subclavate, (0.5)1–2.7(4.3) mm. long; stigmas entire; seeds (1)1.2–1.7(2) mm. long, 0.5–0.7 mm. wide; cotyledons obliquely incumbent, rarely incumbent.

KEY TO THE SUBSPECIES

Petals linear to narrowly oblanceolate, rarely spatulate, 0.5–1.2(3) mm. wide; paired filaments partly to completely united; central and southern Oregon, northeastern California, and southern Washington ..... 9a. subsp. *howellii*.

Petals mostly spatulate, rarely oblanceolate, (1.2)1.5–2.7(3) mm. wide; paired filaments free; eastern Oregon ..... 9b. subsp. *spectabilis*.

9a. **Thelypodium howellii** Watson subsp. **howellii**

Thelypodium howellii Wats., Proc. Amer. Acad. 21:445. 1886. Holotype: Camp Polk, Crook County, Oregon, June 1885, *Thomas Howell 343* (GH).

Streptanthus howellii (Wats.) Jones, Proc. Calif. Acad. Sci., sec. ser., 5:623. 1895.

Thelypodiopsis howellii (Wats.) O. E. Schulz, Bot. Jahrb. 66:98. 1933.

Thelypodium simplex Greene, Pittonia 4:200. 1900. Holotype: adobe meadows, Dixey Valley, Lassen County, California, July 6, 1894, *M. S. Baker & Frank Nutting s.n.* (ND–G); isotype: UC.

Streptanthus coombsae Eastw., Proc. Calif. Acad. Sci., ser. 4, 20: 145. 1931. Holotype: Williamson River, Klamath County, Oregon, July 1913, *A. L. Coombs s.n.* (CAS); isotype: GH.

Basal leaves oblanceolate, mostly lyrately lobed, rarely dentate to entire; petals mostly linear, rarely oblanceolate to spatulate, with the blades usually crisped most of their length, 0.5–1.2(3) mm. wide; paired filaments usually fused most of their length, seldom only fused along their lower third; siliques 1.5–4.6(7) cm. long; plants usually pubescent near the base.

Flowering late May through July at elevations from 3,600 to 5,200 feet in central and southern Oregon, northeastern California, and southern Washington (Map. 2).

REPRESENTATIVE SPECIMENS. **California. Lassen Co.:** 7.3 miles E. of Bieber, *Cantelow 3764* (CAS,DS); **Modoc Co.:** Big Valley, *Baker & Nutting, s.n.*, 1894 (GH, JEPS,POM,UC). **Oregon. Crook Co.:** Big Summit Prairie. Ochoco Mts., between Prineville and Mitchell, T. 14 S., R. 21 E., S. 15, *Cronquist 7461* (GH,NY,UC,WS,WTU); Camp Polk, *Cusick 2812* (F,GH,MO,NY,ORE,POM,UC,US,WS); **Deschutes Co.:** 5 miles below Bend, *Peck 9728* (GH,MO,NY,WTU); **Grant Co.**, near Seneca, *Thompson 11937* (CAS,DS,GH,MO,ND,NY,PH,POM,UC,US,WTU); **Harney Co.:** Silver Creek, *Cusick 2735* (F,GH,MO,ND–G,NY,ORE,POM,RM,UC,US,WS); Harney Valley, *Howell s.n.*, 1885 (DS,F,GH, NA,NY,PH,UC,US,WTU); **Lake Co.:** Paulina Marsh, *Constance 9540* (PH,ORE,WS); Hunters Springs, near Lakeview, *Constance 9541* (ORE,PH); **Klamath Co.:** Harriman Lodge Station, *Abrams 9727* (DS,POM,RM); Swan Lake Valley, *Applegate 30* (DS,GH, US); ½ mile W. of Swan Lake, *Maguire & Holmgren 26562* (COLO,DS,MO,NY,PH,TEX,UC, US,UTC,WS,WTU); Klamath Falls, *Peck 15118* (DS,MO,PH). **Washington. Yakima Co.:** North Yakima, *Leckenby s.n.*, 1898 (WS).

9b. **Thelypodium howellii** Watson subsp. **spectabilis** (Peck) Al-Shehbaz, comb. nov.

Thelypodium howellii Wats. var. *spectabilis* Peck, Torreya 32:150. 1932. Holotype: low alkaline meadow, 10 miles E. of Ironside, Malheur County, Oregon, June 19, 1927, *Morton E. Peck 16066* (not seen); isotype: GH.

Basal leaves oblong-lanceolate to oblong, mostly entire to repand; petals mostly spatulate, rarely oblanceolate, (1.2)1.5–2.7(3) mm. wide, usually crisped between blade and claw; paired filaments free siliques (1.8)3–6.5(8.2) cm. long; plants usually glabrous near the base.

Flowering June through July in eastern Oregon.

REPRESENTATIVE SPECIMENS. **Oregon. Baker Co.:** 3 miles N. of Baker City, *Peck 10416* (DS,NY); **Harney Co.:** Whitehorse Ranch, *Peck 25641* (UC); **Malheur Co.:** 10 miles E. of Ironside on U.S. Hwy. 26, *I. & M. Al-Shehbaz 6957* (GH); **Union Co.:** 1.8 miles N. of jct. U.S. Hwy. 30 and Anthony Lakes road at North Powder, *I & M. Al-Shehbaz 68151* (GH); between Wolf Creek and North Powder, *Howell 28611* (CAS,GH,OSC,WTU).

The one unique feature of *Thelypodium howellii* subsp. *howellii*, that is not present in any other taxon of the genus, is the union of the paired filaments. This character is well-known in the two related genera. *Strep-*

tanthus and *Caulanthus*, but it is far more common in the former. The union of paired filaments in *Thelypodium* was overlooked by Payson (1923), and was first reported by Jepson (1925). In her description of *Streptanthus coombsae*, Eastwood (1931) mentioned this feature of the filaments, but probably was unaware of its occurrence in *T. howellii*. This might have been the main reason for not recognizing the collection she had as a *Thelypodium*, but instead describing it as a *Streptanthus*. The lack of siliques in the type collection lead Morrison (1941) to recognize *S. coombsae* as a good species. He placed it in the subsection *Pulchelli*, section *Euclisia* of *Strepthanthus*. Kruckeberg (1958) questioned its inclusion in this section because of the different habitat in which it grows. We are certain that *S. coombsae* is properly referred to *T. howellii* subsp. *howellii*.

Thelypodium howellii subsp. *spectabilis* is sufficiently distinct from subsp. *howelli* in the general aspects of the petals and filaments that it would be possible to consider it to be a distinct species. However, I have refrained from taking such a position because of the fact that the two subspecies are very similar in their fruiting pedicels, siliques, habit, and cauline leaves.

Of the two subspecies, subsp. *howellii* has a wider distribution, but it appears to be more common in southern Oregon than elsewhere in its range. I have seen four specimens, unquestionably belonging to this taxon, from the state of Washington (one collected by Leckenby in 1898, and three by Vasey in 1889), but these are very old collections and it is possible that the species no longer grows there.

Thelypodium howellii is easily distinguished from the other auriculate-leaved species of *Thelypodium* by its fruiting pedicels that are stout, straight, ascending, often forming a straight line with the siliques; by its lax racemes, ovate to lanceolate-ovate floral buds, and paired filaments that are usually united.

10. **Thelypodium sagittatum** (Nuttall) Endlicher

Herbaceous biennial, or short-lived perennial; stems simple or branched from the base, mostly branched at the inflorescence, glabrous throughout or sparsely to densely hirsute near the base, (2)3–8(12.5) dm. high; basal leaves ovate to oblanceolate, or rarely oblong, obtuse, entire, obtuse to cuneate at base in older leaves, attenuate in younger ones, glabrous or sometimes sparsely pubescent, somewhat thickish, earlier leaves smaller and broader than later ones, (2)6.5–20(29) cm. long, 1–4.2(5) cm. wide; petioles slender, ciliate at least near the base, (1)2–8(14) cm. long; cauline leaves lanceolate to oblong-lanceolate, entire, acute or sometimes acuminate, glabrous or sometimes the lower ones sparsely pubescent along the midrib, occasionally glaucous, somewhat thickish, sagittate to nearly clasping at base, uppermost leaves becoming lanceolate-linear and usually acuminate at apex (0.7)1.6–8.5(14) cm. long, 0.2–1.3(2.8) cm. wide; basal lobes ovate to oblong or lanceolate, obtuse or acute, (1)2–11(23) mm. long, 1–4.5(8) mm. wide; inflorescence densely flowered or lax, racemose to corymbose, strongly elongated in fruit; sepals oblong to ovate-oblong or linear-oblong, obtuse, scarious at margin, slightly to moderately saccate at base, erect, green in the middle and lavender at margin, or purple throughout, (2.5)3–6(10)

mm. long, (1)1.5–2(2.5) mm. wide; petals narrowly to broadly oblanceolate or spatulate, obtuse to subtruncate at apex, white to lavender or purple, sometimes slightly crisped between claw and blade, (5)7–14(19) mm. long, (0.5)1–3(4) mm. wide; claws erect, tapering toward base, (2)3–6.5(10) mm. long; filaments erect, somewhat dilated at base, tetradynamous, white to lavender or purple, filaments of single stamens (2)2.5–4.5(7) mm. long, filaments of paired stamens 3–5.5(8) mm. long; anthers oblong to linear-oblong, sagittate at base, included to partly exserted, (1.5)2–3.2(5) mm. long; glandular tissue well-developed and surrounding base of single stamens, somewhat flat, poorly developed and subtending base of paired stamens or absent; fruiting pedicels slender to stout, straight or more often curved upwards, horizontal to divaricate, or sometimes divaricately ascending, (2.5)5–11(20) mm. long; siliques terete, rarely quadrangular, torulose, straight or somewhat incurved, erect to slightly ascending, slender to stoutish, (1.0)1.3–5.3(6.9) cm. long, (0.5)0.75–1(1.2) mm. wide; styles slender to somewhat stoutish, 0.5–1.5(3.3) mm. long; stigmas entire; gynophores stout, (0.25)0.5–1(2) mm. long; seeds (0.75)1–1.3(1.5) mm. long, 0.5–0.75(1) mm. wide; cotyledons obliquely incumbent, rarely incumbent.

KEY TO THE SUBSPECIES

Petals broadly oblanceolate to spatulate, seldom narrowly oblanceolate, 1–3(4) mm. wide; fruiting pedicels 5–11(20) mm. long; inflorescence corymbose or sometimes racemose; median glandular tissues usually absent; widely distributed ..... 10a. subsp. *sagittatum*.

Petals linear to narrowly oblanceolate, 0.5–1(1.5) mm. wide; fruiting pedicels (2.5)3.5–7(9) mm. long; inflorescence lax raceme; median glandular tissue present; southwestern Utah and adjacent Nevada ..... 10b. subsp. *ovalifolium*.

10a. **Thelypodium sagittatum** (Nuttall) Endlicher subsp. **sagittatum**

Pachypodium sagittatum Nutt. in Torr. & Gray, Fl. N. Amer. 1:97. 1838. Holotype: plains on the west side of the Rocky Mountains, *T. Nuttall s.n.*, 1834 (photo GH of type at BM).

Thelypodium sagittatum (Nutt.) Endl. in Walp. Repert. 1:172. 1842.

Streptanthus sagittatus Nutt., Jour. Acad. Nat. Sci. Phila. 7:12. 1834. Holotype: Little Goddin River (now known as the Little Lost River), Idaho, towards the sources of the Columbia, *N. B. Wyeth s.n.*, 1833 (photo GH of type at BM).

Thelypodium sagittatum (Nutt.) Heller, Bull. Torr. Bot. Club 25:265. 1898 (based on *Streptanthus sagittatus* Nutt.).

Thelypodiopsis sagittata (Nutt.) O. E. Schulz, Bot. Jahrb. 66:99. 1933.

Thelypodium nuttallii Wats., Bot. King's Exped. 26. 1871 (based on *Streptanthus sagittatus* Nutt.).

Thelypodiopsis nuttallii (Wats.) O. E. Schulz, Bot. Jahrb. 66:99. 1933.

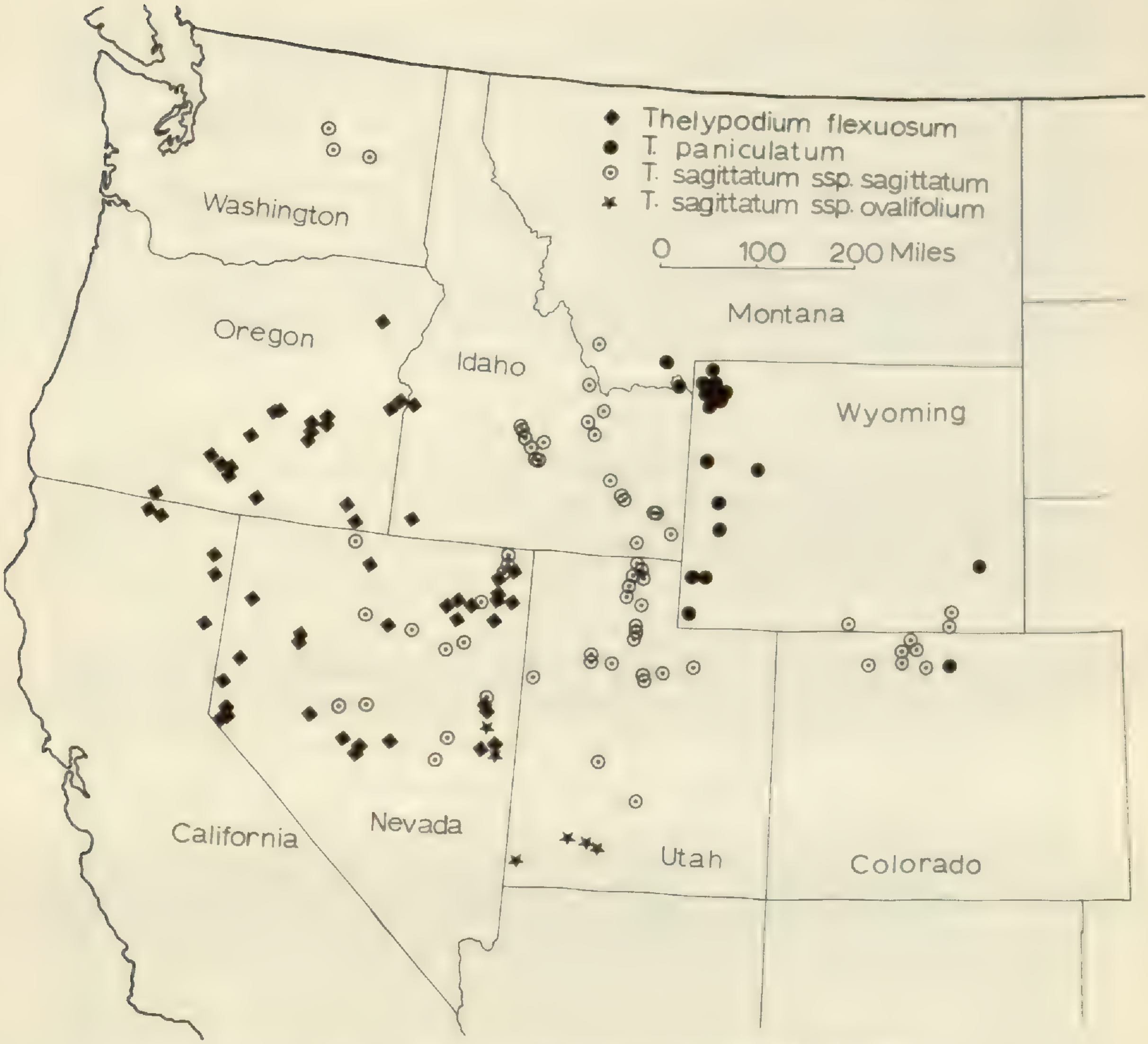
Thelypodium amplifolium Greene, Erythea 4:173. 1896. Lectotype: Hay Ranch, Pine Valley, Nevada, July 25. 1896, *E. L. Greene s.n.* (ND–G); isolectotype: ND–G.

Thelypodium torulosum Heller, Bull. Torr. Bot. Club 25:265. 1898 (based on *Pachypodium sagittatum* Nutt.).

Thelypodiopsis torulosa (Heller) O. E. Schulz, Bot. Jahrb. 66:99. 1933.

Thelypodium macropetalum Rydb., Bull. Torr. Bot. Club 29:233. 1902. Holotype: Farmington, Davis County, Utah, altitude 4,300 feet. May 14, 1881, *Marcus E. Jones 1841* (NY); isotypes: DS,NY,ORE,POM,US,UTC.

Stems simple or branched from the base, with the branches ascending; basal leaves mostly glabrous, petioles ciliate near the base; inflorescence corymbose, sometimes a lax raceme, strongly elongated in fruit; sepals 3–6.5(10) mm. long; petals oblanceolate to spatulate (5)7–14(19) mm. long, 1–3(4) mm. wide; claws 3-6.5(10) mm. long; glandular tissue subtending median stamens usually absent; fruiting pedicels horizontal to divaricate, rarely divaricately ascending to ascending, 5–11(20) mm. long, slender to stout; siliques (1.3)1.8–5.3(6.9) cm. long.



MAP 4. Distribution of *Thelypodium sagittatum*, *T. paniculatum* and *T. flexuosum*.

Flowering early May through July at elevations from 4,300 to 9,000 feet in central and northern Utah, northern Nevada, central Washington, central and southern Idaho, northern Colorado, southern Montana, and southeastern Wyoming (Map 4).

REPRESENTATIVE SPECIMENS. **Colorado. Jackson Co.:** Nelson, *Ripley & Barneby 8996* (CAS); **Routt Co.:** Hayden, *Osterhout 5222* (POM,RM). **Idaho. Bannock Co.:** Pocatello, *Allen s.n.*, 1955 (TEX); **Bear Lake Co.:** 1 mile S. of Bennington, *Christ 14185* (NY); **Bingham Co.:** 5 miles W. of Fort Hall, *Davis s.n.*, 1947 (RSA); **Blaine Co.:** 10 miles N. of Ketchum, *Hitchcock & Muhlick 21359* (COLO,DS,NY,OSC,RM,WS, WTU); **Butte Co.:** 11.2 miles N.W. of Howe, *I. & M. Al-Shehbaz 6919* (GH); **Clark Co.:** Birch Creek, near bridge of Idaho Hwy. 28 at Blue Dome, *I. & M. Al-Shehbaz 6918* (GH); **Caribou Co.:** 3 miles W. of Soda Springs, *Christ 16110* (NY); **Franklin Co.:** Oxford, *Leonard s.n.*, 1885 (DS,GH,NY,POM,RM,UC); **Lemhi Co.:** 10 miles E. of Gilmore, *Hitchcock 15769* (WTU). **Montana. Beaverhead Co.:** Grasshopper Valley, *Watson 39* (GH,US). **Nevada. Elko Co.:** 12.5 miles N. of Contact on U.S. Hwy. 93, *I. & M. Al-Shehbaz 68101* (GH); O'Neil, *Nelson & Macbride 2085* (GH,MO,NY,RM,US,UTC, WTU); **Eureka Co.:** Palisade, *Jones 3768* (CAS,MO,NY,POM,UC,US,UTC); **Humboldt Co.:** 4 miles E. of McDermitt, *Ripley & Barneby 9385* (CAS,NY,UTC); **Lander Co.:** 44 miles

W. of Austin, *Goodner & Henning 645* (NA); **Nye Co.:** vicinity of Currant, *Bently s.n.*, 1916 (DS,POM,RM); **White Pine Co.:** 30 miles W. of Ely, *Delameter s.n.*, 1947 (DS,RSA). **Utah. Box Elder Co.:** Brigham, *Smith 2121* (CAS,NA,NY,RM,UTC); **Cache Co.:** 1½ miles W. of Logan Air Port, *Muenscher & Maguire 2328* (GH,POM,RM,UC,UTC); **Davis Co.:** Bountiful, *Cottam s.n.*, 1938 (UT); **Duchesne Co.:** between Hanna and Rock Creek, *Cottam 9020* (UT); **Millard Co.:** W. of Meadow, near hot springs, *McMillan 1448* (RSA,UT); **Salt Lake Co.:** Crystal Lakes, *Garrett 2929* (NY,UC); **Tooele Co.:** Stansbury Island, *Leonard s.n.*, 1883 (DS,GH,NY,UC); **Utah Co.:** Springville, *Harrison 6503* (MO,US); **Wasatch Co.:** Daniels Canyon, *Garrett 7683* (F,UT); **Wayne Co.:** near Loa, *Jones 5649C* (POM,US). **Washington. Douglas Co.:** W. of Leahy, *Daubenmire 59217* (WS); **Grant Co.:** Coulee City, *Piper 3883* (GH,NY,US,WS); **Lincoln Co.:** near Plum, *Thompson 9146* (US,WTU). **Wyoming. Albany Co.:** Tie Siding, *Stevenson 108* (US); **Carbon Co.:** N. of Baggs, *Osterhout 3196* (RM).

In no other species of *Thelypodium* has the nomenclature been more confused than in *T. sagittatum*. As stated by Payson (1923), this confusion has resulted from the attempts of various taxonomists to maintain both *Streptanthus sagittatus* and *Pachypodium sagittatum* of Nuttall as distinct species. It is very likely that Nuttall himself considered the two to be distinct species, because he did not mention anything about *S. sagittatus* in his original description of *P. sagittatum*. Moreover, he cited a different collection for *P. sagittatum* which was published later. The statement that Nuttall may have considered *P. sagittatum* as a change of the generic status of *S. sagittatus*, as indicated by Payson (1923), does not have any support. Furthermore, the recognition of the two as distinct species by Watson (1871), Robinson (1895), Heller (1898), and a number of other taxonomists argue against Payson's position. The types of the two "species," as judged from their photos at the Gray Herbarium, show slight differences in the size of their flowers, cauline leaves, and auricles as well as differences in the orientation of their pedicels. However, such differences fall easily within the general range of variation of *Thelypodium sagittatum*. In his treatment of the genus *Streptanthus*, Gray (1864) excluded *S. sagittatus* and regarded it as a synonym of *T. sagittatum*, but this disposition of *S. sagittatus* has unfortunately been overlooked.

Thelypodium nuttallii, a name proposed to accommodate the transfer of *Streptanthus sagittatus* to *Thelypodium*, originally represented a very heterogeneous assemblage as judged from the collections cited by Watson. This was clearly pointed out by Robinson (1895) in the following words: "A species of considerable variability as interpreted by Dr. Watson, but difficult to render more definite, owing to Nuttall's brief description and fragmentary type." *Thelypodium sagittatum*, as interpreted by Watson (1871), was even more heterogeneous, since he included collections that not only belong to *T. sagittatum* but also to *T. flexuosum* and *Thelypodiopsis elegans*.

Heller (1898) mishandled the nomenclature by arguing that the specific epithet *sagittatus*, first used in *Streptanthus*, should be retained upon

transfer to *Thelypodium*, and that a new name *(T. torulosum)* should replace *T. sagittatum* (Nutt.) Endl., an earlier transfer to *Thelypodium*, that was based on *Pachypodium sagittatum*. Such an action by Heller was not in accordance with the present code of nomenclature.

The type specimen of *Thelypodium sagittatum* must be the one collected by Nuttall. This is contrary to Payson's (1923, p. 268) typification. He considered *Pachypodium sagittatum* to be a mere transfer of *Streptanthus sagittatus* to *Pachypodium* and not a newly published species. Therefore, he incorrectly assumed that the type specimen of *S. sagittatus*, collected by Wyeth, was also the type of *T. sagittatum*.

Subspecies *sagittatum* as recognized in the present treatment is somewhat heterogeneous. However, any attempt to give taxonomic recognition to even some of the leading variants would not be of real help because most of these variants are neither well-defined morphologically nor do they have a geographical basis. The most variable characters in this subspecies are petal shape, flower size, inflorescence length, silique length, and pedicel length and orientation.

10b. **Thelypodium sagittatum** (Nuttall) Endlicher subsp. **ovalifolium** (Rydberg) Al-Shehbaz, comb. nov.

Thelypodium ovalifolium Rydb., Bull. Torr. Bot. Club 30:253. 1903. Holotype: Panguitch Lake, Garfield County, Utah, alt. 8,400 feet, September 7, 1894, *Marcus E. Jones 6015E* (US); fragments from the type at NY,POM.

Thelypodium palmeri Rydb., Bull. Torr. Bot. Club 34:432. 1907. Holotype: Southern Utah, 1877, *E. Palmer* 25 (NY); isotypes: GH,MO,NA,NY,US. According to an unpublished "Miscellaneous Plant List" in the Gray Herbarium Library, this collection was made from Beaver Valley near Rio Creek.

Stems simple or more often branched from the base, with the branches often subdecumbent; basal leaves glabrous or pubescent, petioles moderately to densely ciliate; inflorescence a lax raceme, slightly elongated in fruit; sepals 3–4.5(5) mm. long; petals oblanceolate-linear or narrowly oblanceolate, 5–7.5(8.5) mm. long, 0.5–1(1.5) mm. wide, claws 2–3.5(4) mm. long; median glandular tissue present; fruiting pedicels divaricately ascending or sometimes ascending to divaricate, stout to slender, (2.5)3.5–7(8) mm. long; siliques 1–3(3.8) cm. long.

Flowering late May through mid August at elevations from 6,000 to 8,400 feet in southwestern Utah and adjacent Nevada.

REPRESENTATIVE SPECIMENS. **Nevada. White Pine Co.:** Duck Creek, *Jones s.n.*, 1893 (POM); 2 miles E. of junction U.S. Hwys. 50 & 93, Becky Spring, *Train 3890* (NA). **Utah. Garfield Co.:** Panguitch Lake, between cabins and road, *I. & M. Al-Shehbaz 6911 & 6984* (GH); Bryce Canyon National Park, *Eastwood & Howell 766* (CAS); **Iron Co.:** Sec. 13, T. 33 S., R. 7 W., *Gierisch s.n.*, 1936 (UTC).

Thelypodium sagittatum subsp. *ovalifolium* shows some variation in the pubescence of the basal leaves and in silique length. These characters were used by Rydberg (1923) to distinguish *T. ovalifolium* from *T. palmeri*. However, the present writer has collected both glabrous and

pubescent forms that also varied considerably in silique length within the same population. The basal leaves in subsp. *ovalifolium* are only ovate at early stages of rosette growth, becoming oblanceolate to spatulate at later stages. This is usually the case in subsp. *sagittatum*, *T. paniculatum*, and to a lesser extent in *T. flexuosum*.

In his treatment of *Thelypodium*, Payson (1923) recognized *T. ovalifolium* as a species distinct from *T. sagittatum*. In fact, he considered it more closely related to and derived from *T. howellii* (p. 243). The only evident resemblance between these two is the presence of lax racemose inflorescences. However, subsp. *ovalifolium* is perfectly at home in *T. sagittatum*, if other characters are taken into consideration. Furthermore, corymbose as well as lax racemose inflorescences are found in subsp. *sagittatum*. Finally, these two subspecies are essentially indistinguishable in their mustard oil contents, and both are very distinct from *T. howellii* (see section on chemistry).

Thelypodium sagittatum often has been confused with certain auriculate-leaved species of *Arabis*, particularly *A. drummondii*, but these two species have nothing in common other than superficial resemblances in their cauline leaves and similar inflorescences. *Thelypodium sagittatum* is sometimes confused with the species originally described as *T. elegans*. The latter species belongs, however, to the genus *Thelypodiopsis* which can be easily distinguished from *Thelypodium* by its bilobed stigma that has the lobes opposite the replum.

The indications that *Thelypodium sagittatum* is present in Oregon (Davis, 1952; Peck, 1961) and California (Hitchcock, 1964) apparently are in error. The present writer has not seen a single specimen of this species from these two states.

Thelypodium sagittatum is readily distinguished from most other auriculate-leaved species of *Thelypodium* by a combination of the following characters: anthers mostly included, filaments tetradynamous, inflorescence a corymbose to lax raceme, fruiting pedicels horizontal to divaricate, and usually erect siliques. From *T. flexuosum*, which is somewhat related, *T. sagittatum* is distinguished by its ciliate petioles, erect, rigid, leafy, and non-flexuous stems, and the lack of a perennial caudex that is covered with petiolar remains of basal leaves. The characters that distinguish *T. sagittatum* from its close relative *T. paniculatum* will be discussed under the latter species.

11. **Thelypodium paniculatum** Nelson

Thelypodium paniculatum Nels., Bull. Torr. Bot. Club 26:126. 1899. Holotype: Fossil, Lincoln County, Wyoming, June 12, 1898, *Aven Nelson 4673* (RM); isotypes: GH,MO,NY,US.

Thelypodiopsis paniculata (Nels.) O. E. Schulz, Bot. Jahrb. 66:99. 1933.

Thelypodium sagittatum (Nutt.) Endl. var. *crassicarpum* Pays., Ann. Mo. Bot. Gard.

9:269. 1923. Holotype: Yellowstone National Park, Yellowstone Canyon, Wyoming, August 24, 1899, *Aven Nelson & Elias Nelson 6663* (MO); isotypes: GH,NY,RM,US.

Plants biennial or short-lived perennial; stems erect, simple or branched at base, mostly branched above, glabrous or seldom sparsely hirsute-hispid near the base, glaucous throughout, solid, (1.4)2–6.5(7.5) dm. high; basal leaves glaucous and often glabrous, mostly oblanceolate, sometimes oblong or spatulate, obtuse to rarely acute, entire, attenuate or occasionally cuneate at base, (3)6–15(22) cm. long, (0.6)1–2.5(4) cm. wide; petioles ciliate at or near the base, slender, (0.8)2–4(6.5) cm. long; cauline leaves glaucous, glabrous or rarely pubescent along midribs, obtuse to acute, oblong to lanceolate-oblong or lanceolate, becoming linear-lanceolate to narrowly lanceolate above, entire, somewhat ascending, mostly sagittate to nearly clasping at base, (1.7)2.2–6(9) cm. long, (0.3)0.5–1.5(3) cm. wide; basal lobes ovate to oblong or occasionally lanceolate-oblong, obtuse to slightly acute, (1)3–8(11) mm. long, 1–3(5) mm. wide; inflorescences corymbose, usually densely flowered, strongly elongated in fruit; sepals oblong to ovate-oblong, obtuse, scarious at margin, lavender to purple, slightly to moderately saccate and unequal at base, erect, (3)3.5–5(6) mm. long, (1)1.5–2 mm. wide; petals broadly spatulate to obovate or broadly obovate, obtuse to sometimes nearly subtruncate, attenuate at base, lavender to purple, not crisped, (6.5)8–11.5(14) mm. long, 2.5–5(6) mm. wide; claws erect, (2)2.5–4(5) mm. long; filaments erect, tetradynamous, filaments of single stamens (2)2.5–4(5) mm. long, filaments of paired stamens (3)3.5–5(6) mm. long; anthers ovate to oblong-ovate, sagittate at base, included, 1–2 mm. long; glandular tissue continuous and disc-like, subtending base of paired stamens, well-developed and surrounding base of single stamens; fruiting pedicels slender to somewhat stout, horizontal to divaricate, or less often divaricately ascending, often slightly curved upwards, rarely straight, somewhat flattened at base, 6–11.5(17) mm. long; siliques terete, stout, slightly torulose, glabrous, somewhat glaucous before drying, erect to somewhat ascending, often slightly incurved, sometimes straight, (1.1)1.3–3.2(5.0) cm. long, (1.3)1.5–2.3 mm. wide; styles slender, (0.5)1–1.7(3) mm. long; stigmas entire; gynophores stout, 0.5–0.75(1.2) mm. long; seeds plump, (1.3)1.5–2 mm. long, 0.75–1 mm. wide; cotyledons obliquely incumbent, rarely incumbent.

Flowering mainly from early June through July at elevations from 6,000 to 9,000 feet in western Wyoming, but mainly in northwestern Wyoming, Idaho and Montana; disjunct in northern Colorado (Map 4).

REPRESENTATIVE SPECIMENS. **Colorado. Larimer Co.:** Camp Creek, *Gooding 1466* (COLO,DS,GH,MO,NY,PH,RM,UC,US). **Idaho. Fremont Co.:** Henry's Lake, *Davis s.n.*, 1935 (RM,UTC). **Montana. Madison Co.:** Alaska Basin, *A. & E. Nelson 5474* (GH,MO,ND,NY, POM,RM,US). **Wyoming. Fremont Co.:** ca. 24 miles S.W. of Dubois near upper end of Warm Springs Creek, Wind River Range, *C. & M. Porter 7530* (DS,NY,RM,RSA,UC,UTC); **Lincoln Co.:** Kemmerer, *Nelson 7164* (NY,RM,US); **Platte Co.:** Wheatland, *Nelson s.n.*, 1891 (RM); **Sublette Co.:** 20 miles W. of Big Piney, *E. & L. Payson 2647* (RM); Horse Creek, W. of Merna, *E. & L. Payson 2741* (RM); **Teton Co.:** Jackson Hole, *Hayden s.n.*, 1860 (MO); Bacon Creek, *Nelson 922* (MO,ND–G,NY,RM,US); **Uinta Co.:** Evanston, *Nelson 4545* (RM); Yellowstone National Park; Alum Creek, Hayden Valley, *I. & M. Al-Shehbaz 6976* (GH); Swan Lake Flat, *Davis 5391* (UC,WS,WTU); Gibbon River, *Hawkins 410* (US); Base of Bunsen Mountain, about 6 miles S.E. of Mammoth Hot Springs, *Rollins & Davis 57193* (GH,MICH,MO,NY,UC); Pelican Creek, *Tweedy 573* (GH,NY).

Thelypodium paniculatum is a relatively invariable species. The characters that are slightly variable, aside from the vegetative parts, are the silique and petal width. The populations of southwestern Wyoming have somewhat narrower siliques and petals than those of Yellowstone National Park and adjacent areas.

In contrast with the majority of species of *Thelypodium*, *T. paniculatum* is less sharply defined. It resembles its closest relative, *T. sagittatum*, in a number of morphological features. The two species have often been confused, and certain taxonomists who have dealt with them, including Payson, maintained a single species. However, Payson (1923) recognized the material from northwestern Wyoming and adjacent areas as a variety *(crassicarpum)* distinct from the rest of *T. sagittatum* on the basis of its having broader siliques. Although the type collection of *T. paniculatum*, collected from southwestern Wyoming has no mature siliques, there is no doubt that a single auriculate-leaved taxon, distinct from the typical *T. sagittatum*, is present in western Wyoming. Whether this distinct taxon is considered to be a variety of *T. sagittatum* or as a distinct species is a matter of judgment. In the present treatment, the rank of species is favored, based on a number of morphological, ecological, and chemical characteristics.

The single collection cited from Colorado *(Goodding 1466)* is disjunct from the main distribution center of the species. There is no doubt that this collection belongs here, since it is indistinguishable from the typical plants of *Thelypodium paniculatum* from northwestern Wyoming. It is not certain whether its presence in Colorado is the result of a recent introduction by man or whether it is a relict of a previous wider distribution.

Thelypodium paniculatum can be easily distinguished from its nearest relative *T. sagittatum* on the basis of its wider petals and siliques, larger and plump seeds, and median glandular tissue that is almost always present. In *T. sagittatum* the petals and siliques are usually narrower, the seeds are somewhat flattened and smaller, and the median glandular tissue, with the exception of subsp. *ovalifolium*, is mostly absent.

Meadows and stream bottoms that remain wet for most of the season appear to be the most favorable sites for *Thelypodium paniculatum*. The present writer has collected it from two localities in Yellowstone National Park, where it was growing in very wet sedge meadows. Dr. Rollins (personal communication) has made the same observation in a different locality. *Thelypodium sagittatum*, on the other hand, favors alkaline meadows that are often dry, but may be wet in the early part of the season. Such differences in the habitat of the two species were first pointed out by Nelson (1899), but were neglected by subsequent taxonomists who dealt with the two species.

The two species are extremely different in their mustard oil contents. As discussed above, the presence of two unique oxazolidine-2-thione producing glucosinolates in *Thelypodium sagittatum* and their absence in *T. paniculatum*, and the presence of the 3-butenylglucosionlate as the dominant constituent in the latter species and its total absence from the former species, besides other differences, clearly stand against the idea of merging the two species.

Thelypodium paniculatum does not appear to occur in Washington. Payson (1923) cited one collection from that state (*Vasey 194*) under *T. sagittatum* var. *crassicarpum*, but the collection is, without question, *T. howellii* subsp. *howellii*.

12. **Thelypodium flexuosum** Robinson

Thelypodium flexuosum Robins. in Gray, Synop. Fl. N. Amer. 1:175. 1895. Holotype; near Carson City, Nevada, 1865, *C. L. Anderson 140* (GH).

Plants perennial; tap roots woody, rather long; caudex woody, simple or branched, covered with papery petiole remains of previous years; stems few to several from the caudex, slender, weak, somewhat flexuous, subdecumbent or less often erect to ascending, solid, few-leaved to nearly naked above, glabrous and somewhat glaucous, mostly branched at the inflorescence, 1.5–5.6(8) dm. high; basal leaves several, glabrous and somewhat glaucous, petioled, mostly lanceolate, sometimes oblong to oblanceolate, rarely ovate, acute to obtuse, entire, cuneate to attenuate at base, somewhat thickish, (2)3.5–16.4(20.5) cm. long, (0.5)1–2.6(4.5) cm. wide; petioles slender, not ciliate, persistent at the base, 1–6.5(13) cm. long; cauline leaves few, linear to lanceolate-linear or lanceolate, acute to acuminate at apex, sagittate to somewhat clasping at base, entire, glabrous and somewhat glaucous, much reduced above, ascending, 1–7(11) cm. long, 2–7(14) mm. wide; basal lobes linear to lanceolate-linear or lanceolate, acute to obtuse, 1–9(14) mm. long, 0.5–2(2.5) mm. wide; inflorescence corymbose, few-flowered, elongated in fruit; sepals oblong to narrowly oblong, obtuse, somewhat scarious at margin, erect, green in the middle and white at margin, somewhat saccate, 3–4(4.5) mm. long, 1–1.5(1.75) mm. wide; petals mostly spatulate or sometimes oblanceolate to obovate, lavender to white, obtuse, not crisped, 6–9(10) mm. long, (1.5)2–3(3.5) mm. wide; claws erect, 2–3.5(4) mm. long; filaments erect, somewhat tetradynamous, filaments of single stamens 2–3.5(4) mm. long, filaments of paired stamens 3–4(5) mm. long; anthers oblong, sagittate at base, included or seldom partly exserted, 1–2(2.5) mm. long; glandular tissue surrounding base of single stamens, low, usually with a lateral extension between the gynophore and petal insertions, median tissue absent; fruiting pedicels slender, straight to slightly curved, horizontal to divaricate, sometimes divaricately ascending, slightly flattened at base, (2.5)4–9(16) mm. long; siliques terete, torulose, straight to slightly curved, erect to ascending, 1.1–2.5(4.2) cm. long, 0.75–1(1.5) mm. wide; styles slender, (0.3)1–2(3) mm. long; stigmas entire, smaller than the diameter of style; gynophores 0.2–0.5(1) mm. long; seeds uniseriate, wingless, non-mucilaginous, brown, faintly reticulate, oblong, (1)1.3–1.5 mm. long, 0.5–0.75(1) mm. wide; cotyledons obliquely incumbent to incumbent.

Flowering late April through June at elevations from 3,000 to 8,000 feet in northeastern California, Oregon, Nevada, and western Idaho (Map 4).

REPRESENTATIVE SPECIMENS. **California. Lassen Co.:** Dokin Unit, Honey Lake Valley, *Anderson s.n.*, 1963 (CAS); **Modoc Co.:** Surprise Valley, *Lemmon s.n.*, 1879 (GH); **Siskiyou Co.:** shore line of Lower Klamath Lake, *Parker 26* (DS,GH,RSA,UC,WTU). **Idaho. Owyhee Co.:** near Battle Creek Ranch, between Riddle and Triangle, *Piemeisel 31–83* (NA); **Payette Co.:** 6 miles S.W. of Fruitland, *Christ 9425* (NY). **Nevada. Churchill Co.:** between Buffalo Canyon and Ione Valley, *Mills & Beach C–87* (UC); **Douglas Co.:** 5 miles S. of Carson City, *Train 3547* (GH,NA,NY); **Elko Co.:** 20 miles S. of Wells, *Holmgren 942* (DS,NA,NY,UC,UTC); 20 miles S.E. of Elko, *Holmgren 1118* (DS,NA,NY,UTC); **Humboldt Co.:** Paradise Valley, *Kennedy 1057* (RM); **Lander Co.:** 10 miles E. of Battle Mountain, *Eastwood & Howell 165A* (CAS,POM); **Nye Co.:** vicinity of Reese River Ranger Station, *Maguire & Holmgren 25485* (DS,GH,NY,UC,US,

UTC,WTU); **Pershing Co.:** 5 miles N. of Oreana, *Train 28* (GH,NA); **Washoe Co.:** Empire City, *Jones 3771* (CAS,DS,NY,POM,UC,US,UTC); **White Pine Co.:** near Connor's Station, *Eastwood & Howell 9363* (CAS,DS,F,GH,POM,WS). **Oregon. Harney Co.:** 21 miles N. of Frenchglen, *Hitchcock & Muhlick 21198* (DS,NY,RM,WS,WTU); between Suntex and Riley, *Maguire & Holmgren 26486* (COLO,DS,MO,NY,UC,UTC,WS,WTU); **Klamath Co.:** White Lake, W. of Merrill, *Applegate 3481* (DS,F,GH,UC,WS); **Lake Co.:** 5 miles S.E. of Paisley, *Hitchcock 6763* (DS,MO,NY,POM,UC,UTC,WS,WTU); 2 miles S. of jct. U.S. Hwy. 395 and Silver Lake Road, *Steward & Smith 7120* (CAS,DS,NY,OSC,UTC, WS,WTU); **Malheur Co.:** about Vale, *Henderson 8445* (CAS,ORE); 40 miles from Fields on road to Crooked Creek Springs, *Hitchcock & Muhlick 22292* (DS,NY,OSC,RM,UC,UT, WS); **Union Co.:** near Medical Springs, *Gale 263* (DS).

Thelypodium flexuosum grows primarily on moderately to strongly alkaline sandy-loam or clayish soils of open deserts. It is unique in the genus in being a weak-stemmed perennial that survives by its thick and woody base. The weak, slender, nearly leafless stems derive their support by being tangled among desert shrubs.

The charcters that readily distinguish *Thelypodium flexuosum* from other auriculate-leaved species of the genus are: woody caudex covered with petiole bases of previous years' growth, persistent basal leaves that wither only after the fruits are dry, petioles that are glabrous, stems that are weak, slender, and usually somewhat flexuous.

Although *Thelypodium flexuosum* is fairly widely distributed, it is probably one of the least variable species in the genus. The basal leaves, cauline leaves, and auricles vary in size as in other species, but the variation in the length of the siliques and the size of the flowers is much less than in the related *T. sagittatum*. The degree of branching of the caudex and its size are sometimes variable within a given population, but this is probably due to the differences in the age of the different plants.

13. **Thelypodium wrightii** Gray

Plants biennial, glabrous and somewhat glaucous throughout; stems erect, simple or rarely branched from the base, paniculately branched above, (1.5)3.2–16.3(28) dm. high; basal leaves lanceolate to sometimes oblanceolate in outline, somewhat thickish, acute to obtuse, cuneate at base, mostly lyrate to pinnately lobed, usually sinuate or dentate near the tip, rarely entire, (6.5)9.5–22.5(28) cm. long, 2.8–5.5(7.5) cm. wide; lobes linear to oblong to deltoid, acute, entire or denticulate, (0.5)0.9–2.5(3.2) cm. long, 0.5–1.8 (2.7) cm. wide; petioles glabrous, (2)4.5–8.5(13.7) cm. long; cauline leaves short petioled, ascending, lanceolate to linear-lanceolate, acute or more often acuminate, entire to dentate or sinuate, sometimes laciniate to pinnately lobed near the base, 3.5–8.8 (13.5) cm. long, 0.7–1.4(2.3) cm. wide, lowermost cauline leaves resembling the basal leaves in their morphology; inflorescence densely flowered, corymbose or short racemose, strongly elongated in fruit; sepals mostly linear-oblong, sometimes oblong or linear, green in the middle and white at margin, or white to lavender throughout, obtuse, scarious at margin, entire, equal and not saccate at base, spreading to mostly horizontal at anthesis, sometimes moderately to strongly reflexed, (3)4–6(7) mm. long, (0.75)1–1.3(1.5) mm. wide; petals white or rarely lavender, not crisped, 4–7.5(9) mm. long, 1–1.75(2) mm. wide, blades mostly oblong, sometimes oblong-linear or linear, usually spreading at anthesis; claws ascending, somewhat dilated at base, 1–2(3) mm. long; filaments white or rarely lavender, equal in length or sometimes slightly tetradynamous, somewhat dilated at base, spreading at anthesis, (3)3.5–6.5(8.5) mm. long; anthers oblong to linear-oblong, exserted, sagittate at base,

(1)1.5–2.5(3) mm. long; glandular tissue continuous, low or sometimes elevated, subtending base of paired stamens, surrounding base of single stamens, usually flat, or sometimes 6-toothed, with the teeth extending between bases of filaments; infructescence mostly congested, or sometimes lax; fruiting pedicels slender to nearly filiform, slightly flattened at base, often faintly striate, mostly divaricate, sometimes horizontal or variously reflexed, rarely divaricately ascending, straight to curved, occasionally grouped on one side of the rachis, (5)7–13(17) mm. long; siliques flattened parallel to septum or more or less terete, torulose, straight to somewhat curved, often horizontal to reflexed, occasionally divaricate, rarely divaricately ascending, (2.5)3.8–7.4(9) cm. long, 1–1.2(1.5) mm. wide; styles stout, clavate to subclavate, rarely cylindrical, (0.5)0.75–2(3) mm. long; stigmas entire; gynophores stout, 0.2–2(5) mm. long; seeds 0.75–1.3(1.5) mm. long, 0.5–0.75 mm. wide; cotyledons obliquely accumbent, rarely accumbent.

KEY TO THE SUBSPECIES

Gynophores 0.25–0.75(1) mm. long; siliques (3.8)4–7.4(9) cm. long; plants of Texas, Arizona, New Mexico, and northern Mexico ..... 13a. subsp. *wrightii*.
Gynophores (1.5)2–4(5) mm. long; siliques (2.5)3–4.8(5) cm. long; plants of northwestern Oklahoma and southeastern Colorado ..... 13b. subsp. *oklahomensis*.

13a. **Thelypodium wrightii** Gray subsp. **wrightii**

Thelypodium wrightii Gray, Smiths. Contrib. (Pl. Wright.) 3:7. 1852. Holotype: Pass of the Limpia, Jeff Davis County, Texas, August 1849, *Charles Wright 7* (GH); isotypes 2GH,US.

Stanleyella wrightii (Gray) Rydb., Bull. Torr. Bot. Club 34:435. 1907.

Glandular tissue low, more or less evenly developed, seldom slightly pointed between filament bases; siliques divaricate to horizontal or reflexed, rarely divaricately ascending, straight or occasionally incurved, (3.8)4–7.4(9) cm. long; gynophores obsolete, 0.25–0.75(1) mm. long.

Flowering mid-June through October, known to flower at earlier dates in Baja California (late March, *Harbison 14846*). Distributed in southwestern Texas, New Mexico, Arizona, and central to northern Mexico (Map 5) at elevations from 2,000 to 8,500 feet.

REPRESENTATIVE SPECIMENS. **Arizona. Apache Co.:** Salina coal mine, *Deaver 3898* (CAS); **Cochise Co.:** road to Rustler Park, Chiricahua Mts., *Goodman & Hitchcock 1208* (CAS,F,GH,MICH,MO,PH,RM,UC); **Coconino Co.:** Bright Angel Trail, Grand Canyon National Park, *I. & M. Al-Shehbaz 6992* (GH); Cosnino, *Jones 4051* (GH,NY,POM,UTC); **Gila Co.:** 10 miles N.W. of Pine, *Wolf 2448* (CAS,GH,POM,RSA); **Maricopa Co.:** near Saddle Mt., T. 7 N., R 8 E., Tonto National Forest, *Little 4151* (NA); **Mojave Co.:** Mt. Trumbull, Grand Canyon National Monument, *Cottam 14069* (GH,UT); 2 miles below headquarters of Hualapai Mountain Park, *Tucker 3500* (CAS,GH,LA,UC); **Yavapai Co.:** Jerome, *Jones 269* (GH,UC). **New Mexico. Catron Co.:** Mogollon Mts., near West Fork of Gila River, *Metcalfe 385* (GH,NMC,NY,UC); **Colfax Co.:** near Cimarron, *Munz 13285* (POM,UC,UTC); **Dona Ana Co.:** Filmore Canyon, Organ Mts., *Wooton s.n.*, 1895 (NY); **Grant Co.:** Gallina's Canyon, *Pilsbury s.n.*, 1915 (PH,POM); **Lincoln Co.:** Gray, *Skehan 42* (GH,ND–G,NMC,NY,POM); White Mts., *Wooton 194* (DS,GH,NMC,NY,POM,UC); **Los Alamos Co.:** Frijoles Canyon, *Macelline 2214* (F); **Luna Co.:** Florita Mts., *Jones s.n.*, 1903 (POM); **McKinley Co.:** Fort Wingate, *Matthews 6* (GH); **Rio Arriba Co.:** El Rito picnic ground, Carson National Forest, 7 miles N. of El Rito, *Nelson 470* (UC); **Sandoval Co.:** Jemez Springs Canyon, *Nelson 11627* (GH, UC); **San Miguel Co.:** vicinity of Las Vegas, *Ancet 284* (GH); **Santa Fe Co.:** Cañoncito, *Arséne 15918* (UC); **Socorro Co.:** Bear Mts., *Greene s.n.*, 1880 (F,ND–G,NY,PH,POM);

Torrance Co.: Manzano Mts., N.W. of Manzano, *Barneby 12851* (CAS). **Texas. Brewster Co.:** Paisano Pass campground, about 10 miles W. of Alpine on Hwy. 90, *Correll 34106* (GH); Chisos Mts., Big Bend National Park, *Mueller 8003* (F,NY,TEX); **Culberson Co.:** 30 miles N. of Van Horn, Sierra Diablo Mts., *Correll 31617* (GH); **El Paso Co.:** near Hueco Tanks, Hueco Mts., *Waterfall 6624* (GH,NY); **Hudspeth Co.:** Victoria Canyon, Sierra Diablo Mts., about 20 miles N. of Allamore, *Waterfall 5384* (GH); **Jeff Davis Co.:** Limpia Canyon, 11 miles N.E. of Fort Davis, *Lundell 13136* (UC); Davis Mt., *Palmer 31839* (NY,PH,POM); **Presidio Co.:** San Esteban Lake, 12 miles S. of Marfa, *Hinkley s.n.*, 1940 (GH). **Utah. Garfield Co.:** Marvine Loccolite, *Jones s.n.*, 1894 (POM). **Mexico. Baja California:** Santa Catarina, 64 miles S.E. of Ensenada, *Broder 330* (US); San Matias Pass, near Diablito Spring, Valle de la Trinidad, *Harbison 14846* (DS); road N. of Sam's Corral, 31°04′ N, 115°34′ W, Sierra San Pedro Mártir, *Moran 14538* (GH); Cantillas Mts., *Orcutt 945* (F,GH,NA,UC); **Chihuahua:** road from Castillón to Mula, hills near Poza de Villa, 3 miles W. of Coahuila line, *Johnston & Muller 1387* (GH); near Chihuahua, *Pringle 294* (F,GH,NA,NY,PH,RSA); Cañon de la Madera, S. E. flank of Sierra Rica, *Stewart 2500* (GH); **Coahuila:** vicinity of San José, S.E. base of Sierra de las Cruces, *Johnston & Muller 985* (GH); canyon at San Antonio de los Alamos, Sierra de San Antonio, *Johnston & Muller 886* (GH); 2–10 miles N. of camp at La Noria, Sierra del Pino, *Johnston & Muller 594* (GH); Sierra del Carmen, Canyon de Sentenela on Hacienda Piedra Blanca, *Wynd & Muller 621* (GH,NY); **Hidalgo:** Cerro Grande, S.E. of Epazoyucan, *Rzedowski 29325* (GH).

13b. **Thelypodium wrightii** Gray subsp. **oklahomensis** Al-Shehbaz, subsp. nov.

Siliquis erectis vel adscendentibus, rectis vel incurvatis, (2.5)3–4.8(5) cm. longis; stipite tenui vel crasso, (1.5)2–4(5) mm. longo.

Holotype in the Gray Herbarium, collected among rock crevices, 4 miles E. of Kenton, Cimarron County, Oklahoma, August 18, 1950, *G. J. Goodman & R. W. Kelting* 5358; isotypes: COLO,NY,RSA,TEX,WTU.

Glandular tissue continuous, usually 6-toothed, paired teeth conspicuous or reduced, united near the base. inserted between base of single filaments and gynophore, up to 0.75 mm. high, single teeth inserted between and outside base of paired stamens; siliques erect to ascending, sometimes divaricately ascending, rarely divaricate, often strongly incurved, rarely straight, (2.5)3–4.8(5) cm. long; gynophores slender or rarely stout, (1.5)2–4(5) mm. long.

Flowering late July through early October in northwestern (panhandle) Oklahoma and southeastern Colorado. This subspecies was first reported from Oklahoma by Goodman (1936) as *Stanleyella wrightii.*

REPRESENTATIVE SPECIMENS. **Colorado. Baca Co.:** Sand and Gallinas canyons, 27 miles S. of Pritchett, T. 35 S., R. 48 W., Sec. 5 & 8, *Weber 4322* (COLO); 4 miles N. of Oklahoma line, N. of Kenton, *Rogers 6432* (COLO); **Chaffee Co.:** Salida, *Harper s.n.*, 1886 (WIS); **Fremont Co.:** Canyon of the Arkansas, 18 miles S.W. of Canyon City, *Waterfall 10888* (RSA); **Las Animas Co.:** Trinidad, *Osterhout 5755* (RM). **Oklahoma. Cimarron Co.:** John Regnier Ranch, Kenton, *Demaree 13386* (GH,NY); 3 miles E. of Kenton, *Goodman 2287* (CAS,GH,NY).

Thelypodium wrightii grows primarily on clay-loam to sandy-loam soils that are usually moist. It is often found in sheltered areas of oak-woodlands or pinyon-juniper associations along rocky slopes, cliffs, and ledges of canyons and river banks.

The characters that are most variable in *Thelypodium wrightii* are leaf margin, length and orientation of fruiting pedicels and siliques, length of

the inflorescence, and density of siliques in the infructescence. These characters are, by and large, variable within a given population, and do not seem to fall in any particular geographical patterns.

Thelypodium wrightii, as discussed before, was the basis for establishing the genus *Stanleyella* by Rydberg mainly on the grounds of its having spreading instead of erect sepals as in the majority of *Thelypodium* species. However, systematists working with the Cruciferae realize how insignificant such a character can be. The only other character, found in *T. wrightii*, that is not common in *Thelypodium* is the shape of the style, which is clavate to subclavate. However, this type of style characterizes two other species, *T. laxiflorum* and *T. repandum*, that also have spreading sepals and it occurs sporadically in other species, including *T. laciniatum*.

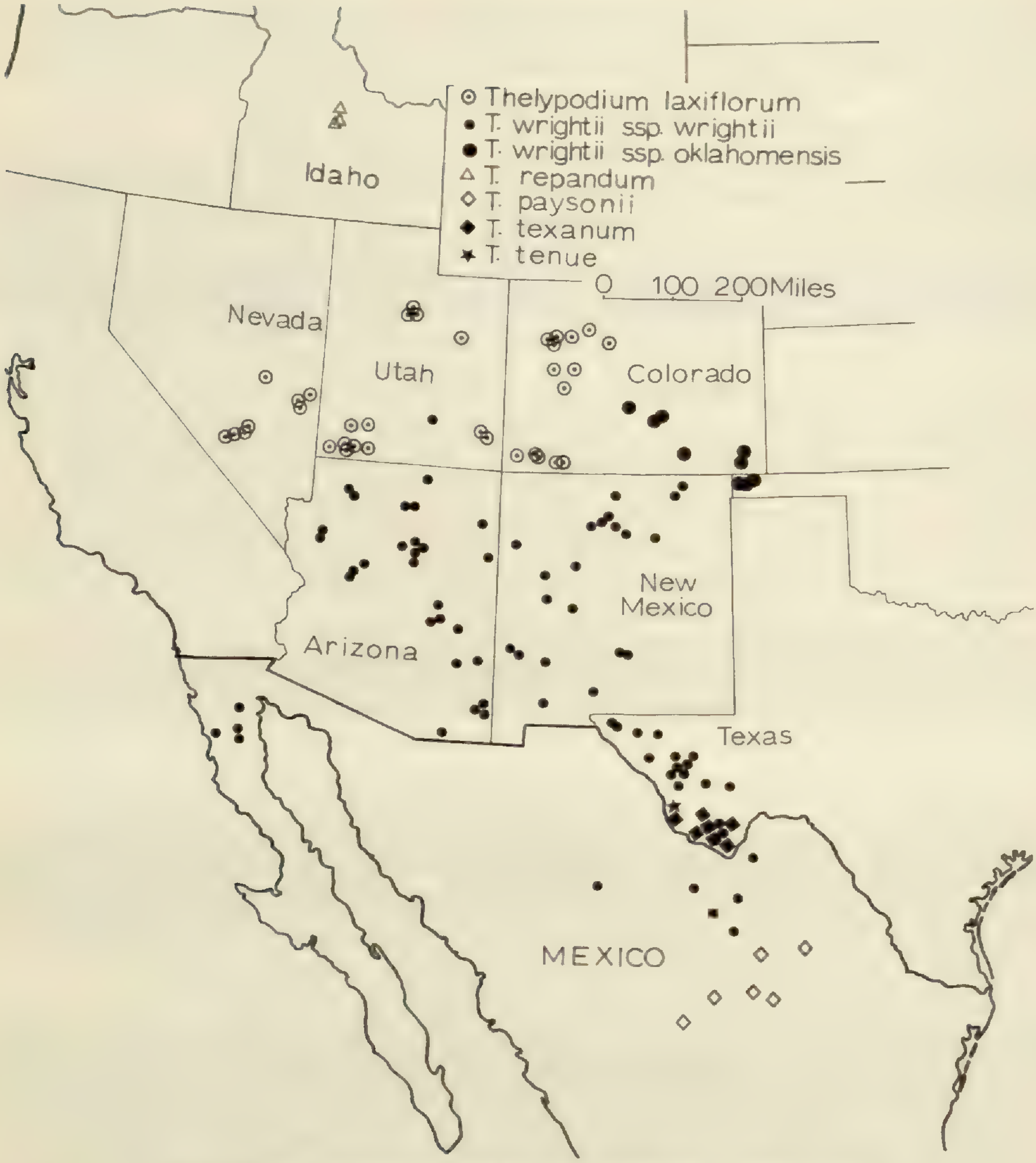
In his treatment of *Thelypodium* and its immediate allies, Payson (1923) stated that the filaments are folded in the floral buds of *T. wrightii* (as *Stanleyella*). However, the present writer failed to detect such a character in any of the materials studied, including herbarium specimens as well as living material in the field and greenhouse. *Thelypodium wrightii* was said to be present in Colorado and Utah by Payson (1923), Rydberg (1923), and Tidestrom and Kittell (1941), but the plants these authors were referring to are placed in *T. laxiflorum* in the present treatment. Kearney and Peebles (1960) reported *T. wrightii* from Pinal, Pima, and Greenlee Counties of Arizona, but I have not seen specimens from these counties. I have found no reason to question the correctness of their identifications, but it is not known where the specimens they used are presently located.

Until recently, the distribution of *Thelypodium wrightii* in Mexico was thought to be restricted to the northern portions of the country. Dr. Rollins has kindly brought to my attention a specimen sent to him by G. C. Rzedowski, who collected it from the state of Hidalgo. This collection certainly expands the distributional range of the species much farther south than what was known before 1973. Whether the species is disjunct in Hidalgo or has a continuous distribution with its range in northern Mexico is not known. The single collection from Utah (*Jones s.n.*, 1894, POM) is somewhat disjunct, but there is no doubt that it belongs here. It is not unlikely that *T. wrightii* will be found in other localities of southern Utah.

14. **Thelypodium laxiflorum** Al-Shehbaz, sp. nov.

Thelypodium wrightii Gray var. *tenellum* Jones, Proc. Calif. Acad. Sci. (ser. 2) 5:622. 1895. Holotype: Slate Canyon, Provo, Utah County, Utah, alt. 6,000 feet, July 2, 1894, *M. E. Jones* 5559 (POM); isotypes: NY,US.

Stanleyella wrightii (Gray) Rydb. var. *tenella* (Jones) Pays., Ann. Mo. Bot. Gard. 9:317. 1923.



Map 5. Distribution of species of *Thelypodium* with spreading sepals.

Herba biennis; caulibus ramosis, farctis, inferne hispidis-hirsutis vel glabratis superne glabris, (1.5)3.1–14(23.5) dm. altis; foliis radicalibus petiolatis oblanceolatis, pinnatilobatis vel lyratis, glabris vel sparse pubescentibus, (4)7.2–20.5(30) cm. longis, (0.6)1–4(10) cm. latis; lobis linearibus vel oblongis, integris vel dentatis; foliis caulinis superne linearibus vel lanceolatis, integris vel dentatis, acutis vel acuminatis, 1.5–7(10) cm. longis, 0.3–1.2(2) cm. latis; inflorescentibus corymbosis, laxis; sepalis oblongis, non saccatis, patentibus vel adscendentibus, albis vel lavandulis, (2.5)3–5(5.5) mm. longis, 1–1.75(3) mm. latis; petalis spathulatis vel oblanceolatis, albis vel lavandulis, inferne erectis, 5–7.5(9.5) mm. longis, 1.5–2.5(3.5) mm. latis; staminibus erectis, tetradynamis, 2.5–4.5(5.5) mm. longis; antheris sagittatis, inclusis, (1) 1.5–2.2(2.5) mm. longis; pedicellis fructiferis tenuibus, divaricatis vel reflexis, (4)5–13(19) mm. longis; siliquis stipitatis, teretibus, tenuibus, submoniliformibus, divaricatis vel reflexis, rectis vel curvatis, (2)3–6.6(7.4) cm. longis, 0.75–1(1.5) mm. latis, stylis clavatis, (0.5)0.75–2(5) mm. longis; stigmatibus parvis, integris; seminibus exalatis, oblongis, uniseriatis; cotyledonibus oblique incumbentibus.

Holotype in the Gray Herbarium, collected on sandy soil along roadside, ca. 2 miles east of Glenwood springs, Garfield County, Colorado, June 3, 1968, *Larry C. Higgins 1487;* isotypes to be distributed.

Plants biennial; stems simple or sometimes branched from the base, branched at the inflorescence, sparsely to densely hirsute or hirsute-hispid below, or glabrous throughout, (1.5)3.1–14(23.5) dm. high; basal leaves petiolate, mostly oblanceolate, acute to obtuse, often pinnately to lyrately lobed, rarely laciniate or sinuate, glabrous and somewhat glaucous, or sparsely pubescent, (4)7.2–20.5(30) cm. long, (0.6)1–4(10) cm. wide; lobes linear to oblong, rarely deltoid, entire or dentate, acute, divisions between lobes extending to midrib and becoming gradually shallower toward leaf apex, 0.3–2.2(6.5) cm. long, 2–9(18) mm. wide; petioles glabrous or sparsely to densely hirsute-hispid, (1)1.7–8(11) cm. long; upper cauline leaves short petioled, ascending, glabrous, linear to linear-lanceolate or lanceolate, sometimes oblanceolate or oblong, sinuate to dentate, occasionally entire or repand, rarely lobed near the base, acute to acuminate, 1.5–7(10) cm. long, 0.3–1.2(2) cm. wide; inflorescence few flowered, corymbose, somewhat lax, greatly elongating in fruit; sepals white or sometimes lavender, oblong, obtuse, slightly scarious at the margin, spreading or, more often, ascending, non-saccate, equal at base, (2.5)3–5(5.5) mm. long, 1–1.7(3) mm. wide; petals white or rarely lavender, mostly spatulate, sometimes oblanceolate or obovate, obtuse to subtruncate at apex, not crisped, erect below and horizontal above, 5–7.5(9.5) mm. long, 1.5–2.5(3.5) mm. wide; filaments white, slightly dilated at base, erect, tetradynamous, filaments of single stamens 2.5–3.5(4.5) mm. long, filaments of paired stamens 3–4.5(5.5) mm. long; anthers oblong, sagittate at base, included to partly exserted, (1)1.5–2.2(2.5) mm. long; glandular tissue uniformly developed, low, surrounding base of single stamens, subtending base of paired stamens; infructescence mostly lax, rarely congested; fruiting pedicels terete, slender, somewhat flattened at base, mostly divaricate, sometimes slightly to strongly reflexed, rarely horizontal or divaricately ascending, (4)5–13(19) mm. long; siliques terete, slender, straight or sometimes curved, submoniliform to strongly torulose, divaricate to variously reflexed, rarely divaricately ascending, (2)3–6.6(7.4) cm. long, 0.75–1(1.5) mm. wide, replum slightly or strongly constricted between the seeds; styles clavate to subclavate, slender to stout, (0.5)0.75–2(5) mm. long; stigmas entire; gynophores stout, 0.5–0.75(1.5) mm. long; seeds (1)1.3–1.75(2) mm. long, 0.5–1 mm. wide; cotyledons obliquely incumbent, rarely incumbent.

Flowering late May to early September at elevations from 4,100 to 9,000 feet in southern Nevada, Utah, and western Colorado (Map 5).

REPRESENTATIVE SPECIMENS. **Colorado. Archuleta Co.:** along trail to Chimney Rock Mesa, Piedra, *Schmoll 1496* (COLO); **Eagle Co.:** road from Dotsero towards Coffee Pot Springs, White River Plateau, *Weber 12049* (COLO); Minturn, *Osterhout 2553* (NY, RM); Wolcott, *Osterhout 4237* (NY,POM,RM); **Garfield Co.:** near Glenwood Springs, *Rollins 57151* (GH); **Gunnison Co.:** road from Kebler Pass towards Somerset, *Gentry 2277* (COLO); Lead King Basin, Crystal, *Langenheim 2120* (COLO); **La Plata Co.:** Durango, *Baker, Earle & Tracy 510* (F,GH,ND–G,NY,POM); **Montezuma Co.:** Spruce Canyon near jct. with Navajo Canyon, *Weber 3628* (CAS,COLO,RSA,TEX); **Pitkin Co.:** Coal Creek Basin, *Langenheim 1432* (COLO). **Nevada. Lincoln Co.:** Panaca, *Jones s.n.*, 1912 (NY,POM); Kershaw Canyon, *Ripley & Barneby 4395* (CAS,GH,NY); Ryan State Park, 4 miles S. of Caliente, *Train 2466* (NA,RSA); **Nye Co.:** southwestern rim of Rainier Mesa, Holmes Road, S.W. end of Belted Range, *Beatley 9426* (GH); tributary of South Silent Canyon, E. of Well 9, N. of Pahute Mesa Road, *Reveal 1238* (GH); Troy Canyon, western base of Troy Mountain, *Sharsmith 4819A* (GH,UC). **Utah. Carbon Co.:** E. of Sunnyside, W. of Tavaputs Plateau, *Welsh & Murdock 9145* (GH); **Iron Co.:** 8.4 miles S.E. of Cedar City on Utah State Hwy. 14, *I. & M. Al-Shehbaz 6912* (GH); **Kane Co.:** E. of Zion National Park, *Rossbach & Hodgdon s.n.*, 1934 (GH); **San Juan Co.:** above Allen Creek, Mt. Linnaeus, Abajo Mts., *Cronquist & N. Holmgren 9487* (NY,WS); **Utah Co.:** Bridal Veil Falls, Provo Canyon, *I. & M. Al-Shehbaz 6879* (GH); **Washington Co.:** Zion National Park, *Thackery 528* (NA,UC).

The ecological counterpart of *Thelypodium wrightii* in Nevada, Utah, and western Colorado is *T. laxiflorum*. The two species inhabit slightly

moist areas that are partly shaded, and sometimes in association with *Populus tremuloides*, scrub oak, Artemisia-Pinyon-Juniper, and others.

Thelypodium laxiflorum exhibits an interesting pattern of stem pubescence. Plants of the populations from Nevada seem always to be glabrous-stemmed, while those from Utah and Colorado are primarily pubescent near the base. However, no taxonomic recognition is given to the populations from Nevada for two reasons. First, the presence or absence of pubescence in the Cruciferae can be under simple Mendelian genetic control, as discovered by Rollins (1958) in the genus *Dithyrea*, and second, both glabrous and pubescent forms were found within the same population in a number of localities.

Plants of *Thelypodium laxiflorum* were placed in *T. wrightii* by earlier workers, who overlooked the significant differences in the flowers and siliques. Payson (1923) maintained *T. wrightii* var. *tenellum* (under the segregate genus *Stanleyella*), but cited only the type collection of this variety. He cited a number of collections from Colorado, Utah, and Nevada, that unquestionably belong to *T. laxiflorum* (var. *tenellum sensu* Payson), under *T. wrightii*. As did Jones, Payson recognized that the plants collected from Slate Canyon (the type locality of var. *tenellum*) were different from typical *T. wrightii* in their "delicate" cauline leaves, pubescent stems, and lax infructescences, but he too failed to detect the significant differences in the flowers and siliques (Plate 22). There is no question but that two distinct species exist. The present writer favored the presentation of this taxon as new at the species level rather than making a new combination based on var. *tenellum* whose fragmentary type collection has no flowers.

The series of populations that belong in *Thelypodium laxiflorum* resemble those of the closely related *T. wrightii* in certain morphological features such as leaf shape and margin, fruiting pedicels, glandular tissue, and style shape. However, this is where the significant similarities stop. The flowers and siliques of the two species are very different (Plate 22). In *T. laxiflorum* the sepals are ascending to spreading. The petals are spatulate to oblanceolate, 1.5–2.5(3.5) mm. wide, not sharply differentiated into claw and blade, and with their claw-like lower half almost always erect. The stamens are tetradynamous and erect. The siliques are submoniliform, with the replum variously constricted between the seeds. In *T. wrightii* the sepals are spreading to variously reflexed, the petals spreading and differentiated into claw and blade, with the blades oblong to linear-oblong and 1–1.7(2) mm. wide. The stamens are always spreading and more or less equal in length. The siliques are torulose, with the replum straight and not constricted between the seeds.

15. **Thelypodium repandum** Rollins

Thelypodium repandum Rollins, Contrib. Dudley Herb. 3:371. 1946. Holotype: 20 miles south of Challis, on soft shale cliffs west of Salmon River, Custer County, Idaho,

June 15, 1944, *C. L. Hitchcock & C. V. Muhlick 8985* (DS); isotypes: DS,MO,NY,RSA,UC, WS,WTU.

Plants biennial or short-lived perennial; stems simple or branched at base, usually branched above, fairly robust, glabrous and somewhat glaucous, 1–4.4(6.0) dm. high; basal leaves and lower cauline leaves glabrous and distinctly glaucous, usually gray to bluish-gray, petiolate, rather fleshy, mostly ovate, less often obovate or elliptic, rarely orbicular or spatulate, obtuse to acute, cuneate at base, usually repand and lyrate, sometimes sinuate-repand or dentate, rarely entire, (2.2)4–10.5(14) cm. long, (1) 1.5–4.3(5.5) cm. wide; petioles glabrous, 1–4(6) cm. long; uppermost cauline leaves short-petioled, elliptic or often lanceolate, entire or repand; inflorescence rather densely-flowered, raceme short; sepals purple to lavender, spreading to horizontal at anthesis, oblong, obtuse, somewhat scarious at the margin, not saccate, (2.5)3–4 mm. long, (0.75)1–1.5(1.75) mm. wide; petals purple to lavender, spreading at anthesis, straight, undifferentiated into claw and blade, oblanceolate, rarely spatulate, obtuse, attenuate to claw-like base, not crisped, (2.5)3–4.5 mm. long, 0.5–1 mm. wide; filaments lavender, straight, spreading at anthesis, slightly dilated at the base, equal in length or slightly tetradynamous, 2.5–3.75 mm. long; anthers purple, sagittate at base, slightly exserted, oblong, becoming recurved when fully dehisced, 1–1.75 mm. long; glandular tissue low, evenly developed, surrounding base of single stamens, subtending base of paired stamens; fruiting pedicels straight to somewhat curved, slender, divaricate to divaricately ascending, slightly flattened at the base, 4–12(15) mm. long; siliques narrowly linear, torulose, somewhat flattened parallel to septum, erect to ascending, rarely divaricate, straight or sometimes incurved, rarely recurved, (2)4–7.4 cm. long, 1–1.5(1.75) mm. wide; styles cylindrical to subclavate, 0.5–1.2(1.5) mm. long; stigmas entire; gynophores 0.5–0.75(1) mm. long; seeds (0.75)1–1.5 mm. long, 0.5–0.75 mm. wide; cotyledons obliquely accumbent, rarely accumbent.

Flowering in June at elevations around 5,700 feet in Custer County, Idaho.

REPRESENTATIVE SPECIMENS. **Idaho. Custer Co.:** 8.1 miles S. of Challis on U.S. Hwy. 93, along west facing steep canyon bank of Salmon River, *I. & M. Al-Shehbaz 6921* (GH); 5 miles up South Fork of Salmon River, Stanley-Challis Road, *Hitchcock & Muhlick 10805* (DS,WTU); 8 miles S. of Challis, *Hitchcock & Muhlick 14120* (CAS,DS, F,MO,NA,NY,PH,RM,RSA,UC,UTC,WS,WTU); 20 miles E. of Clayton, *Hitchcock 15674* (WTU); 8 miles E. of Clayton, Salmon River Canyon, *Ripley & Barneby 8837* (GH,NY).

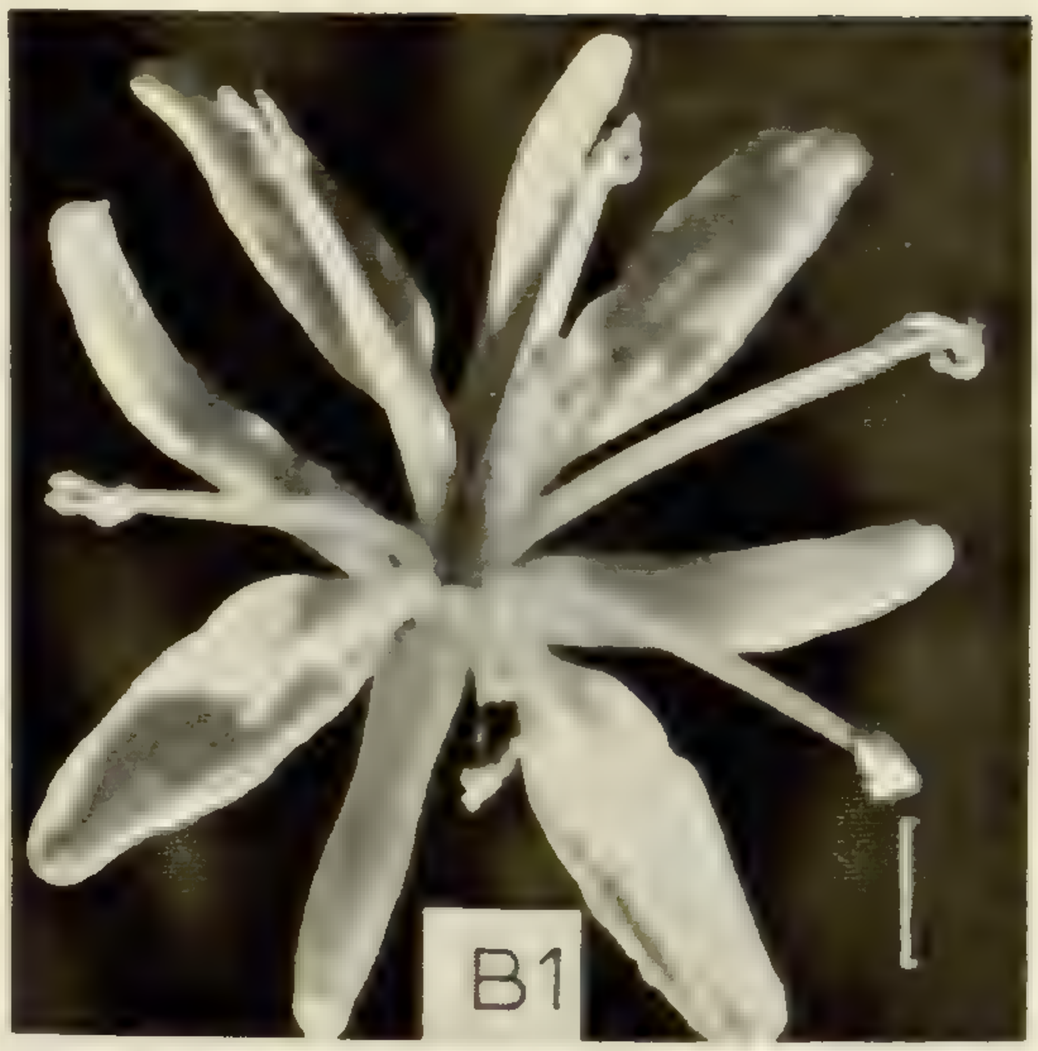
This handsome species is a very narrow endemic, that appears to grow only on decomposing shale banks of the Salmon River and its tributaries in Custer County, Idaho. *Thelypodium repandum* is unquestionably related to the species of *Thelypodium* with spreading sepals, petals, and stamens, but the relationship is remote rather than direct. It is easily distinguished from other species of *Thelypodium* with petiolate cauline leaves by a combination of its small purple to lavender flowers that have spreading parts, and ovate lower leaves that are fleshly and strongly glaucous.

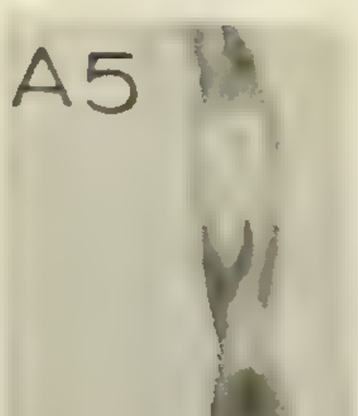
16. **Thelypodium texanum** (Cory) Rollins

Sisymbrium texanum Cory, Rhodora 39:418. 1937. Holotype: Terlingua Creek, 18 miles north of Terlingua, Brewster County, Texas, April 13, 1936. *V. L. Cory 18564* (GH).

Stanleyella texana (Cory) Rollins, Madroño 5:134. 1939.

Thelypodium texanum (Cory) Rollins, Contrib. Dudley Herb. 3:371. 1946.





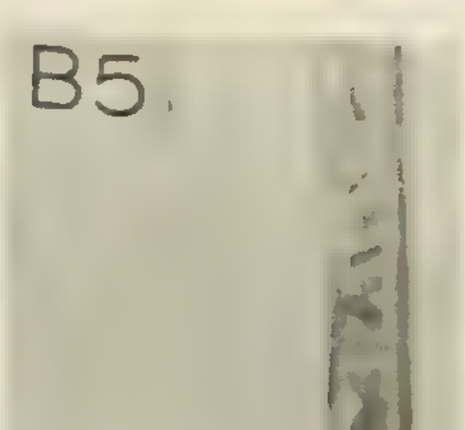


PLATE 22. Flowers and siliques of *Thelypodium laxiflorum* (A) and *T. wrightii* (B). FIG. 1. Flower, top view; FIG. 2. Flower, side view; FIG. 3. Androecium, median view; FIG. 4. Androecium, lateral view; FIG. 5. Replum. Scale: one mm.

Plants annual; stems usually simple or rarely branched from the base, mostly branched above, glabrous and somewhat glaucous, 1.3–4.8(6.1) dm. high; basal leaves and lowermost cauline leaves petiolate, somewhat thickish, oblanceolate or sometimes spatulate in outline, glabrous and glaucous, pinnately lobed to rarely laciniate, acute to nearly obtuse, (3.4)5–15(24) cm. long, (1.1)1.5–3.5(5.5) cm. wide; petioles expanded at base, glabrous, 1–2.5(4) cm. long; lobes (3)5–10(12) on each side, acute to obtuse, mostly oblong, sometimes oblong-lanceolate or ovate, variously dentate, sometimes repand or entire, rarely sinuate, with the upper lobes usually decurrent, smaller and remote on lower portion of the leaf, divisions between lobes usually extending to midrib below and becoming gradually shallower toward leaf apex; uppermost leaves short-petioled, nearly pectinate, with the lobes usually linear; inflorescence a densely flowered raceme, short, greatly elongated in fruit; sepals oblong to linear oblong, obtuse, entire, scarious at margin, green above and white below, or lavender throughout, not saccate, equal at base, spreading or sometimes reflexed at anthesis, usually coiled later at anthesis, (2.5)3–5 mm. long, 1–1.5 mm. wide; petals mostly spatulate or sometimes oblanceolate, not crisped, obtuse, attenuate to claw-like base, straight, spreading at anthesis, white, undifferentiated into claw and blade, (3.5)4–6.5(7) mm. long, (0.5)1–2 mm. wide; filaments equal in length or rarely tetradynamous, white, terete, linear, somewhat dilated at base, spreading at anthesis, (4)4.5–6.5(7) mm. long; anthers purple, sagittate at base, exserted, oblong to linear-oblong, usually coiled when fully dehisced, (1)1.5–2 mm. long; glandular tissue well-developed, disc-like, surrounding base of single stamens, subtending base of paired stamens; fruiting pedicels slender to stoutish, divaricate to horizontal, seldom slightly reflexed, more or less flattened at the base, striate, straight or more often slightly incurved, (4)6–14(17) mm. long; siliques narrowly linear, often divaricately ascending to divaricate, rarely ascending or erect, torulose, flattened parallel to septum, straight or sometimes recurved, (1.9)2.8–6(7.1) cm. long, (1)1.3–1.5(1.7) mm. wide; styles conical to subconical, rarely cylindrical, 0.75–1.5(3) mm. long, stigmas entire; gynophores 0.5–1(2) mm. long; seeds (1)1.25–1.5 mm. long, 0.75–1(1.25) mm. wide; cotyledons mostly obliquely accumbent, rarely accumbent.

Flowering early February through April in southwestern Texas on clay or sandy soil on barren hillsides and gravelly creek beds.

REPRESENTATIVE SPECIMENS. **Texas. Brewster Co.:** Terlingua Beds, 7 miles E. of Lajitas, *Correll 30685* (GH,LL); Tornillo Creek,, near Rio Grande Hot Springs, Big Bend National Park, *Goodman & Waterfall 4609* (COLO,GH,TEX,UC); 65 miles S. of Alpine, *Innes & Warnock 496* (GH,TEX); 2 miles S.E. of Hen Egg Mountains, *Johnston &Warnock 3652* (NY); Cottonwood Creek, Big Bend National Park, *Rollins & Correll 6184A* (GH); Terlingua Creek, 3 miles E. of Terlingua, *Rollins & Correll 6186* (GH); N. of Terlingua turn-off, Texas State Hwy. 118, *Rollins & Correll 6188* (GH); **Presidio Co.:** about 24.5 miles S.E. of Redford, *Correll 30681* (GH,LL); Fresno Creek, 1 mile above Fresno mine, between Fresno Canyon and Rio Grande River, *Rollins & Correll 61106* (GH).

Thelypodium texanum, like *T. tenue*, is endemic to southwestern Texas, but it is certainly far more common than the latter species. It is somewhat variable in the various aspects of its leaves, but aside from the slight variability in fruit orientation and length of pedicels, the species as a whole is only slightly variable in other morphological features.

Like *Thelypodium tenue* and *T. paysonii*, *T. texanum* is a winter annual. The greenhouse plants of the last species took a minimum of 8 to 10 weeks to grow from the seedling to the flowering stage. No dormancy requirements were evident, since mature seeds, removed from plants that were still growing, germinated readily with a high percentage (80–100%).

One interesting feature found in some plants of *Thelypodium texanum* that was not observed in other species of the genus, is the emergence of pistils from the mature floral buds before they open. This is a clear-cut case of protogyny. The significance of this phenomenon has already been discussed under the section on breeding systems.

17. **Thelypodium tenue** Rollins

Thelypodium tenue Rollins, Rhodora 59:64. 1957. Holotype: bed of Fresno Creek, about 1 mile below Smith Mine, Presidio County, Texas, January 25, 1942, *L. C. Hinckley* 2336 (GH).

Herbaceous annual; stem single from the base branched above, glabrous and glaucous, over 3 dm. high; basal leaves and lowermost cauline leaves somewhat thickish, oblanceolate in outline, petiolate, pinnately lobed, glabrous and glaucous, obtuse to acute at apex, 1–2 dm. long, 2–4 cm. wide; lobes acute, irregularly dentate or somewhat sinuate, smaller and remote on lower portion of leaf, decurrent on rachis, divisions between lobes extending to midrib; petioles expanded at the base; uppermost cauline leaves nearly pectinate, with the lobes linear to lanceolate-linear; inflorescence a densely flowered short raceme, elongated in fruit; sepals obtuse, somewhat scarious at margin, greenish to purplish above and white below, not saccate, spreading at anthesis, oblong, 3–5 mm. long, 1–1.5 mm. wide; petals straight, spreading at anthesis, spatulate, not crisped, attenuate at base to short claw, 5–8 mm. long, 1–1.5 mm. wide; filaments spreading at anthesis, white, equal in length or slightly tetradynamous, slightly dilated at base, 5–8 mm. long; anthers purplish, oblong to linear-oblong, sagittate at base, exserted, 2–2.5 mm. long; glandular tissue continuous, subtending base of filaments; pedicels very slender, striate, divaricately ascending, slightly flattened at base, 2–3.5 cm. long; young siliques stipitate, narrowly linear, slightly flattened parallel to septum; styles short, slender; stigmas entire; gynophores short; mature fruits and seeds not seen.

The fact that *Thelypodium tenue* is similar to *T. texanum* in many morphological features of the leaves and flowers is readily shown by comparing specimens of the two species. However, the present writer has seen only the holotype of the former species. Further collections should provide valuable information particularly on fruit morphology, the overall variability in the species, and geographic distribution.

That *Thelypodium tenue* is most closely related to *T. texanum* was clearly pointed out by Rollins (1957a). It is easily distinguished from the other species of *Thelypodium* by its pedicels that are, by far, the longest in the genus (2–3.5 cm. long). Long and slender pedicels are also found in the remotely related *T. wrightii* and *T. laxiflorum*, but they are shorter than those of *T. tenue*.

The shape of the style seems to be a good criterion to group the species of *Thelypodium* with spreading floral parts. Therefore, as suggested by Rollins (1957a), *T. tenue*, *T. texanum*, and *T. paysonii* that have subconical styles are more related to each other than to *T. wrightii* and *T. laxiflorum* which have clavate to subclavate styles. This is supported by other morphological features including growth habit. *Thelypodium repandum* is somewhat exceptional in the sense that it is more related

to *T. texanum* than to *T. wrightii* or *T. laxiflorum* on other morphological grounds, but resembles the last two species in having clavate to subclavate styles as well as being a biennial.

18. **Thelypodium paysonii** Rollins

Thelypodium paysonii Rollins, Rhodora 59:61. 1957. Holotype: Cañon de Jara, east of Socorro, lower part of canyon near its mouth, about 30 km. west of Cuatro Cienegas, Coahuila, Mexico, February 1–15, 1941, *Albert H. Schroeder 12* (GH).

Plants annual; stems solid, slender, simple or branched from the base, always branched above, moderately to densely hirsute below, sparsely hirsute or rarely glabrous above, 0.6–4.7(7) dm. high; trichomes simple, spreading; basal leaves and lower cauline leaves petiolate, pinnately lobed, glabrous to sparsely pubescent along main veins, acute to obtuse, mostly oblanceolate to spatulate in outline, 6.5–20(26) cm. long, 1.8–6(8) cm. wide; lobes narrowly to broadly oblong, rarely ovate or oblong-lanceolate, acute to obtuse, glabrous or rarely ciliate, dentate or sometimes sinuate-dentate, rarely repand or entire, smaller and remote on lower portion of the leaf; petioles slender, mostly pubescent, 2–6(8.5) cm. long; upper cauline leaves reduced, with the lobes linear to lanceolate-linear; inflorescences densely flowered, corymbose, greatly elongated in fruit, rachis usually pubescent; sepals oblong, obtuse, somewhat scarious at the margin, non-saccate, equal at the base, green above and white below, ascending or less often spreading at anthesis, 3–4(4.5) mm. long, (1)1.5–2 mm. wide; petals differentiated into claw and blade, with the blades spatulate to obovate, white, not crisped, obtuse or rarely subtruncate, spreading at anthesis, 4–6(6.5) mm. long, 1–1.5(1.75) mm. wide; claws slender, slightly dilated at the base, covered with short gland-like trichomes on their lower half, 2–3(3.5) mm. long; filaments white, erect, slightly dilated at the base, slightly tetradynamous or nearly equal in length, covered with short gland-like trichomes on their lower third or half, 3–6 mm. long; anthers oblong to linear-oblong, sagittate at base, exserted, coiled when fully dehisced, 1–1.5 (2) mm. long; glandular tissue uniform, low, disc-like, subtending the bases of all filaments; fruiting pedicels slender, slightly flattened at base, glabrous, divaricate to horizontal, rarely divaricately ascending, straight or recurved, (2)6–10(16) mm. long; siliques straight or slightly curved, not torulose, slightly flattened parallel to septum, horizontal or usually pendulous, seldom divaricately ascending, (0.6)2–4.8(5.3) cm. long, (1)1.3–2 mm. wide; styles slender, subconical or less often cylindrical, (0.75)1.5–2.5 mm. long; stigmas entire; gynophores slender, (0.5)1–2.5 mm. long; seeds 1–1.5 mm. long, ca. 1 mm. wide; cotyledons oblique.

Known to flower in November and February in northern Mexico. This variation in flowering dates and growth cycle may well be related to the availability of moisture. The species appears to grow primarily on rocky slopes or canyon walls.

REPRESENTATIVE SPECIMENS. **Mexico. Coahuila:** Monclova, *Palmer 2146* (GH); Torreon, *Purpus 130* (GH,UC); Sierra de Parras, *Purpus 1028* (GH); 44 miles E. of Torreon, *Rollins & Tryon 58296* (GH,MICH,MO,NY,UC,US); **Durango:** 48 miles S.W. of Torreon, *Rollins & Tryon 58291* (GH,MICH,MO,NY,UC).

The specimen collected by Palmer (2146), and identified by Watson as *Sisymbrium*, is different from the other specimens cited above in having much shorter siliques (0.6–2 cm. long) borne on much shorter pedicels (2–5 mm. long) that are straight and divaricate. It may represent an undescribed infraspecific taxon of *Thelypodium paysonii* but I have refrained from describing it because the specimen is too fragmentary.

Thelypodium paysonii is somewhat anomalous in the genus in having non-torulose siliques and pubescent filaments and claws. The characteristic short gland-like trichomes on the lower parts of the filaments and claws serve as an excellent character to distinguish this species from others of the genus. The adaptive significance of these trichomes is not known, but they may help in the accumulation of large drops of nectar in the center of the flower. It is doubtful that they have any secretive function.

Regardless of the "anomalous" features mentioned above, *Thelypodium paysonii* fits within the genus, and appears to be related to the other annual species, *T. texanum* and *T. tenue*. It resembles these species in having pinnately lobed leaves, spreading floral parts, subconical styles, and an annual habit.

Very little is known about the ecology and the overall variability of this interesting species which is unique in a number of features as mentioned above. This is probably due to the fact that the species is a narrow endemic, and that it has been collected only a very few times in the past century as judged from the collections available.

SPECIES EXCLUDED FROM THELYPODIUM OR NAMES OF DOUBTFUL APPLICATION

The types and/or isotypes of the following taxa were seen by the present writer, unless it is otherwise indicated.

1. *Thelypodium ambiguum* Wats., Proc. Amer. Acad. 14:290. 1879. =*Thelypodiopsis ambigua* (Wats.) Al-Shehbaz, comb. nov. (see the discussion under the generic relationships in connection with this species as well as the others placed in *Thelyodiopsis*).

2. *Thelypodium anisopetalum* Greene, Pittonia 3:247. 1897. =*Pennellia longifolia* (Benth.) Rollins, Rhodora 62:16. 1960.

3. *Thelypodium aureum* Eastw., Zoe 2:227. 1891. =*Thelypodiopsis aurea* (Eastw.) Rydb., Bull. Torr. Bot. Club 34:432. 1907.

4. *Thelypodium auriculatum* (Gray) Wats., Proc. Amer. Acad. 17:321. 1882. =*Sisymbrium auriculatum* Gray, Smithson. Contrib. (Pl. Wright.) 3:8. 1852.

5. *Thelypodium australe* Brandeg., Zoe 5:180. 1904. =*Romanschulzia australe* (Brandeg.) Rollins, Contrib. Dudley Herb. 3:225. 1942.

6. *Thelypodium bakeri* Greene, Plantae Bakerianae 3:8. 1901. =*Thelypodiopsis elegans* (Jones) Rydb., Bull. Torr. Bot. Club 34:432. 1907.

7. *Thelypodium cooperi* Wats., Proc. Amer. Acad. 12:246. 1877. =*Caulanthus cooperi* (Wats.) Pays., Ann. Mo. Bot. Gard. 9:293. 1923.

8. *Thelypodium crenatum* Greene, Pittonia 4:20. 1899. =*Lepidium montanum* Nutt. ex Torr. & Gray subsp. *spathulatum* (Robins.) C. L. Hitchc. Madroño 10:158. 1950.

9. *Thelypodium deserti* Jones, Contrib. Western Bot. 12:1. 1908. =*Sibara deserti* (Jones) Rollins, Contrib. Gray Herb. 165:140. 1947.

10. *Thelypodium diehlii* Jones, Contrib. Western Bot. 12:2. 1908. Type collection not seen. This species probably belongs to *Sisymbrium*, since it was suggested by Jones to correspond well to *Thelypodium vaseyi* Coult., which is *S. shinnersii* Johnst. Payson (1922) listed *T. diehlii* as a questionable synonym under *S. wootonii* Robins., but he did not see the type collection either. Whether this is the proper generic position for *T. diehlii* or not remains unsolved, but because of its bilobed stigmas the species does not belong to *Thelypodium* in any case. *Sisymbrium wootonii* may belong to the group of species placed here under *Thelypodiopsis*, but it is not advisable to make any transfer at the present time because mature fruits are not known.

11. *Thelypodium elegans* Jones, Zoe 4:265. 1893. =*Thelypodiopsis elegans* (Jones) Rydb., Bull. Torr. Bot. Club 34:432. 1907.

12. *Thelypodium endlicherianum* Muschl. ex O. E. Schulz in Notizbl. Bot. Gart. Berlin 11:390. 1932. Listed as a synonym of *Arabis endlichii* Schulz (=*Sibara viereckii* (Schulz) Rollins var. *Endlichii* (Schulz) Rollins) but it was not validly published.

13. *Thelypodium flavescens* (Hook.) Jeps., Fl. West. Middle Calif. 212. 1901. =*Caulanthus flavescens* (Hook.) Pays., Ann. Mo Bot. Gard 9:301. 1923.

14. *Thelypodium flavescens* Wats., Bot. King's Exped. 25. 1871. =*Caulanthus flavescens* (Hook.) Pays., Ann. Mo. Bot. Gard. 9:301. 1923.

This species has a long history of confused nomenclature. It is variously known under the generic names *Caulanthus, Streptanthus, Guillenia,* and *Thelypodium.* There is no doubt that the species is at home in *Caulanthus* and not the other genera for the reasons mentioned under the discussion of *Caulanthus.* I have seen the holotype of *Streptanthus dudleyi* Eastw. (Proc. Calif. Acad. Sci., ser. 4, 20:145. 1931.) and *Streptanthus lilacinus* Hoover (Leaflets West. Bot. 1:226. 1936.), and it is clear that they are additional synonyms of *Caulanthus flavescens.*

15. *Thelypodium flexicaule* (Dusén) Gilg & Muschl., Engl. Bot. Jahrb. 42:438. 1909.

This species was transferred from *Sisymbrium* (*S. flexicaule* Dusén, Arkiv. för Botanik 7:22. 1907). The species is a native of Patagonia. I have not seen the type collection, but judging from the description and the illustrations provided, the species does not belong in *Thelypodium.* In fact, in my opinion *Thelypodium* does not occur in South America or Central America. The genus does not occur south of central Mexico. In 1924, Schulz placed *Sisymbrium flexicaule* as a synonym of *Chilocardamum patagonicum* (Speg.) Schulz (based on *Sisymbrium patagonicum* Speg.). Whether the species belongs to *Sisymbrium* or *Chilocardamum* is beyond the scope of the present work.

16. *Thelypodium greenei* Jeps., Fl. West. Middle Calif. 212. 1901. =*Caulanthus flavescens* (Hook.) Pays., Ann. Mo. Bot. Gard. 9:301. 1923.

17. *Thelypodium harmsianum* Muschl., Engl. Bot. Jahrb. 40:267. 1908 =*Polypsecadium harmsianum* (Muschl.) O. E. Schulz, Pflanzenreich 86, (IV, 105): 177. 1924.

The species was based on a collection from southern Bolivia. I have not seen the type collection of this species, but I have seen an isotype of *T. harmsianum* var. *dentata* Muschl. at US that was also collected from southern Bolivia. This species is far from being close to *Thelypodium* because it has very broadly bilobed stigmas (with the lobes opposite the replum), non-torulose siliques, and very small flowers that are quite different from those of any known species of *Thelypodium.* As mentioned before, neither *Thelypodium* nor any member of the tribe *Thelypodieae* occurs in the southern hemisphere. Schulz (1924) placed this species in the monotypic genus *Polypsecadium.*

18. *Thelypodium harmsianum* var. *dentata* Muschl., Engl. Bot. Jahrb. 40:268. 1908. =? *Polypsecadium harmsianum* var. *dentatum* (Muschl.) Schulz, Pflanzenreich 86, (IV, 105): 177. 1924.

19. *Thelypodium hookeri* Greene, Fl. Franciscana 263. 1891. =*Caulanthus flavescens* (Hook.) Pays., Ann. Mo. Bot. Gard. 9:301. 1923.

20. *Thelypodium jaegeri* Rollins, Contrib. Dudley Herb. 3:174. 1941.

In his description of *T. jaegeri,* Rollins (1941a) pointed out the differences between this species and those belonging to *Thelypodium* proper. He adopted the broadly defined concept of *Thelypodium,* because of the fact that the generic lines were not satisfactorily established between the various species that were placed in *Thelypodium* at one time or another. In the present treatment, *T. jaegeri* is excluded for a number of reasons. First, and as noted by Dr. Rollins, the lack of basal leaves forming a well-defined rosette and the presence of caespitose and a suffruticose habit in *T. jaegeri* are not known in any species of *Thelypodium.* Second, the siliques are mostly non-torulose in *T. jaegeri,* with the stigmas as wide or wider than the style, while in all species of *Thelypodium* (except *T. paysonii*) the siliques are torulose and the stigmas almost always smaller than the diameter of the style. Finally, the median sepals are wider than the lateral ones in *T. jaegeri,* while they are narrower or as wide as the lateral sepals in all species of *Thelypodium.* It is beyond the scope of the present study to place this species in some other genus, but we are certain that it does not belong in *Thelypodium.*

21. *Thelypodium lasiophyllum* (Hook. & Arn.) Greene, Bull. Torr. Bot. Club 13: 142. 1886. =*Caulanthus lasiophyllus* (Hook. & Arn.) Pays., Ann. Mo. Bot. Gard. 9:303. 1923. (See the discussion under *Caulanthus*.)

22. *Thelypodium lasiophyllum* (Hook. & Arn.) Greene var. *inalienum* Robins. in Gray, Synop. Fl. N. Amer. 1:177. 1895. =*Caulanthus lasiophyllus* (Hook. & Arn.) Pays. var. *inalienus* (Robins.) Pays., Ann. Mo. Bot. Gard. 9:306. 1923.

23. *Thelypodium lasiophyllum* (Hook. & Arn.) Greene var. *rigidum* (Greene) Robins. in Gray, Synop. Fl. N. Amer. 1:177. 1895. =*Caulanthus lasiophyllus* (Hook. & Arn.) Pays. var. *rigidus* (Greene) Pays., Ann. Mo. Bot. Gard. 9:307. 1923.

24. *Thelypodium lasiophyllum* (Hook. & Arn.) Greene var. *utahense* (Rydb.) Jeps., Man. Fl. Pl. Calif. 413. 1925. =*Caulanthus lasiophyllus* (Hook. & Arn.) Pays. var. *utahensis* (Rydb.) Pays., Ann. Mo. Bot. Gard. 9:307. 1923.

25. *Thelypodium lasiophyllum* (Hook. & Arn.) Greene f. *xerophilum* (Fourn.) Thell. Mitt. Bot. Mus. Zürich 83:735. 1919. =*Caulanthus lasiophyllus* (Hook. & Arn.) Pays.

26. *Thelypodium lemmoni* Greene, West. Amer. Sci. 3:156. 1887. =*Caulanthus anceps* Pays., Ann. Mo. Bot. Gard. 9:303. 1923. (See the discussion under *Caulanthus*.)

27. *Thelypodium linearifolium* (Gray) Wats., Bot. King's Exped. 25. 1871. =*Thelypodiopsis linearifolia* (Gray) Al-Shehbaz, comb. nov.

28. *Thelypodium lobatum* Brandeg., Univ. of Calif. Publ. Bot. 4:178. 1911. =*Sisymbrium auriculatum* Gray, Smithson. Contrib. (Pl. Wright.) 3:8. 1852.

O. E. Schulz (1924) recognized *lobatum* as a variety of *Coelophragmus auriculatus* (Gray) Schulz. However, neither *lobatum* nor *Coelophragmus* are worth recognition. *Sisymbrium auriculatum* is a perfectly good *Sisymbrium*. Moreover, *Coelophragmus*, as defined by Schulz, contained another species *C. umbrosus* (Robins.) Schulz (based on *Sisymbrium umbrosum* Robins.), which is without doubt a synonym of *Dryopetalon runcinatum* Gray. This was shown to be so by Rollins (1941b).

29. *Thelypodium longifolium* (Benth.) Wats., Bot. King's Exped. 25. 1871. =*Pennellia longifolia* (Benth.) Rollins, Rhodora 62:16. 1960.

30. *Thelypodium longifolium* var. *catalinense* Jones, Contrib. West. Bot. 12:2 1908. =*Pennellia micrantha* (Gray) Nieuw., Amer. Midl. Nat. 5:224. 1918.

31. *Thelypodium longirostris* (Wats.) Jeps., Man. Fl. Pl. Calif. 413. 1925. =*Streptanthella longirostris* (Wats.) Rydb., Fl. Rocky Mts., 364. 1917.

32. *Thelypodium macrorrhizum* Muschl., Engl. Bot. Jahrb. 40:268. 1908.

This is another of those species from South America that were originally described in *Thelypodium* by Muschler and later transferred to monotypic genera by Schulz (1924). In this case, *T. macrorrhizum* was placed in a genus of its own called *Phlebiophragmus* Schulz, which was said to be different from *Sisymbrium* in having a septum with 2–4 nerves instead of being nerveless, 1-nerved, or 2-nerved. It is very doubtful that such a character is significant enough to call for the erection of a monotypic genus. It may be possible to place this species in *Sisymbrium* without any radical change of the generic limits. In fact, *T. macrorrhizum* was transferred to *Sisymbrium* by Macbride (S. *macrorrhizum* (Muschl.) Macbr., Candollea 5:355. 1934).

33. *Thelypodium mexicanum* Brandeg., Zoe 5:179. 1904. =*Romanschulzia australe* (Brandeg.) Rollins, Contrib. Dudley Herb. 3:225. 1942.

34. *Thelypodium micranthum* (Gray) Wats., Proc. Amer. Acad. 17:321. 1882. =*Pennellia micrantha* (Gray) Nieuw., Amer. Midl. Nat. 5:224. 1918.

35. *Thelypodium neglectum* Jones, Amer. Nat. 17:875. 1882. =*Caulanthus lasiophyllus* (Hook. & Arn.) Pays., Ann. Mo. Bot. Gard. 9:303. 1923.

36. *Thelypodium pallidum* Rose, Contrib. U.S. Nat. Herb. 8:294. 1905. =*Romanschulzia arabiforme* (DC.) Rollins var. *lasiocarpa* (Schulz) Rollins, Contrib. Dudley Herb. 3:222. 1942.

37. *Thelypodium petiolatum* Hemsl., Diagn. Pl. Nov. Mex. 2. 1878. =*Iodanthus petiolatus* (Hemsl.) Rollins, Contrib. Dudley Herb. 3:211. 1942.

This species was placed by Schulz (1924) in a genus of its own named *Chaunanthus*. The fact that it belongs in the same genus as *Iodanthus pinnatifidus* was clearly shown by Rollins (1942a). Schulz (1936) not only maintained *Iodanthus* and *Chaunanthus*, but he placed each of them in a different tribe.

38. *Thelypodium pinnatifidum* Wats., Bot. King's Exped. 25. 1871. =*Iodanthus pinnatifidus* (Michx.) Steud., Nom. Bot. ed. 2, pt. 1:812. 1840.

39. *Thelypodium procerum* (Brewer) Greene, Fl. Franciscana 263. 1891. =*Caulanthus flavescens* (Hook.) Pays., Ann. Mo. Bot. Gard 9:301. 1923.

40. *Thelypodium purpusii* Brandeg., Zoe 5:232. 1906. =*Sisymbrium purpusii* (Brandeg.) O. E. Schulz, Pflanzenreich 86, (IV, 105): 58. 1924.

41. *Thelypodium rigidum* Greene, Pittonia 1:62. 1887. =*Caulanthus lasiophyllus* (Hook. & Arn.) Pays. var. *rigidus* (Greene) Pays., Ann. Mo. Bot. Gard. 9:307. 1923.

42. *Thelypodium* (?) *salsugineum* (Pall.) Robins. in Gray, Synop. Fl. N. Amer. 1:175. 1895. =*Sisymbrium salsugineum* Pall., Reise Prov. Russ. Reich. II. App. 740. no. 114, t. 5, 1773.

43. *Thelypodium stamineum* Eastw., Leaflets West. Bot. 2:7. 1937. =*Caulanthus pilosus* Wats., Bot. King's Exped. 27. 1871.

44. *Thelypodium suffrutescens* Rollins, Ann. Carnegie Mus. 26:224. 1937. =*Glaucocarpum suffrutescens* (Rollins) Rollins, Madroño 4:233. 1938.

45. *Thelypodium tularense* Jones, Contrib. West. Bot. 18:21. 1935. Type not seen, but judging from the description, this "species" may well prove to be a synonym of *Caulanthus lasiophyllus* (Hook. & Arn.) Pays.

46. *Thelypodium utahense* Rydb., Bull. Torr. Bot. Club 29:233. 1902. =*Caulanthus lasiophyllus* (Hook. & Arn.) Pays. var. *utahensis* (Rydb.) Pays., Ann. Mo. Bot. Gard. 9:307. 1923.

47. *Thelypodium vaseyi* Coult., Contrib. U.S. Nat. Herb. 1:30. 1890. =*Sisymbrium shinnersii* Johnst., Southwestern Nat. 2:129. 1957.

48. *Thelypodium vernale* Woot. & Standl., Contrib. U.S. Nat. Herb. 16:128. 1913. Several attempts to locate the type specimen of this species in the U.S. National Herbarium have failed, but judging from the description and the absence of the auriculate-leaved species of *Thelypodium* in New Mexico, this species appears to be a *Sisymbrium*. In fact, it was transferred to *Sisymbrium* by Schulz (Pflanzenreich 86, [IV, 105]: 57. 1924). This may prove to be the right treatment if the species is indeed a good one.

49. *Thelypodium versicolor* Brandeg., Univ. Calif. Publ. Bot. 4:178. 1911. =*Sisymbrium versicolor* (Brandeg.) Schulz, Pflanzenreich 86, (IV, 105): 57. 1924.

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PURPLE-FLOWERED ARABIS OF THE PACIFIC COAST OF NORTH AMERICA

Reed C. Rollins

The genus *Arabis* (Cruciferae) is well-represented in the flora of western North America. Some species are abundant and widespread while others are very restricted in distribution, often being confined to specialized habitats and/or soil types. In my treatment of the genus in North America west of the hundredth meridian (Rollins, 1941), I recognized 53 species together with a number of infraspecific taxa. Since then, names for several additional taxa that occur in the same area have been published (Boivin, 1951; Rollins, 1946, 1971). Our present concern is with one of the evolutionary "bursts" within *Arabis* which has resulted in a group of related species found in the hills, mountains and coastal areas of northern California and southern Oregon. The most spectacular feature shared by these species is a comparatively large and conspicuous lavender to purplish flower. This feature, coupled with that of a rosette (usually flattened) of obovate to broadly oblanceolate leaves from which the fertile stems arise marks these species as being distinctive among the American members of the genus. The known species involved are *A. aculeolata, A. blepharophylla, A. mcdonaldiana, A. modesta,* and *A. oregana.* None of these are widespread in occurrence. Presumably the most restricted, *A. mcdonaldiana,* is known from but a single locality. In 1942, Lincoln Constance and I hiked to this site at the summit of "Big" Red Mountain southeast of Bell Springs in northern Mendocino County, California. There we found *A. mcdonaldiana* growing abundantly on red serpentinized soil in open areas between such shrubs as *Arctostaphylos, Ceanothus prostratus,* and *Quercus vaccinifolia.* A few days before, we had collected *A. aculeolata* at four different locations in Josephine County, Oregon and in at least two instances the site was a serpentine barren. More recent collections of these purple-flowered species show that serpentine soils figure prominantly in the habitat of at least three of the species. Adaptation to serpentinized soils or at least the reduced competition provided by such sites as in the genus *Streptanthus* (Kruckeberg, 1951, 1969) appears to be a significant factor involved in the speciation of the group. The need for a careful and detailed study of the situation in this respect is clearly indicated. Additional field research in the area would be rewarding.

Some further evidence suggesting a highly local occurrence of this type of *Arabis* which is at the same time associated with outcrops of serpentine rocks comes from added new material. In 1971, Chester A. Ground sent to me for determination specimens collected on a serpentine ridge of the south slope of Preston Peak in northern Siskiyou County, California. Although obviously related to *A. aculeolata,* these specimens appeared to

be a sample of an undescribed taxon but they were without mature fruit. During the field season of 1972, Mr. Ground and Gilbert J. Muth were able to collect a number of specimens of the same taxon in various stages of maturity. From these, it is evident that an undescribed species is indeed represented. In order to provide a quick guide for those wishing to distinguish among the species of this purple-flowered group, the following key is presented.

A. Seeds wingless; plants glabrous throughout ..... 1. *A. serpentinicola.*
A. Seeds winged at least distally; plants pubescent or hirsute (*A. mcdonaldiana* with only a few simple trichomes on teeth of basal leaves).
B. Seeds oblong; winged primarily at the distal end; siliques 4–6 cm. long, 1.5–2 mm. wide, acute at apex; Napa and Yolo Counties, California northward to southern Oregon.
C. Plants low, less than 1.5 dm. high, glabrous except for a few marginal trichomes on basal leaves; petals 2.5–3 mm. wide; usually truncate .... 3. *A. mcdonaldiana.*
C. Plants taller, 2–5 dm. high, hirsute or pubescent at least below; petals 4–8 mm. wide, rounded at apex.
D. Trichomes simple, forked or three-pronged at apex of long stalk, large with bulbous base; leaves ciliate; stems coarsely hirsute with spreading trichomes, rarely glabrous.
E. Leaf trichomes simple; basal leaves dentate, narrowly obovate, densely rosulate, 1–2.5 cm. long, 0.5–1 cm. wide; stems several from a closely branching caudex ..... 2. *A. aculeolata.*
E. Leaf trichomes forked or rarely three-pronged at apex; basal leaves usually entire, broadly obovate, loosely rosulate to erect, 2–5 cm. long, 1–2.5 cm. wide; stems one or few from a simple or loosely branched caudex ..... 4. *A. oregana.*
D. Trichomes dendritically branched with a short stalk, comparatively small without a bulbous base; leaves uniformly pubescent without a ciliate margin; stems with appressed several-rayed trichomes ..... 5. *A. modesta.*
B. Seeds orbicular, winged all around; siliques 2–3 cm. long, 2–3 mm. wide, obtuse at apex; primarily coastal or in the outer coast ranges from Sonoma County to Santa Cruz County, California ..... 6. *A. blepharophylla.*

1. **Arabis serpentinicola** Rollins, sp. nov.

Herba perennis, glabris, caulibus simplicibus erectis 1.5–3 dm. altis, foliis basilaribus glabris obovatis crassis rosulatis 1.5–2.5 cm. longis, 1–1.5 cm. latis, foliis caulinis sparsis sessilibus non auriculatis 3–6 mm. longis, sepalis purpureis oblongis 4.5–5.5 mm. longis, petalis spathulatis purpureis 12–15 mm. longis, pedicellis divaricatis 4–8 mm. longis, siliquis divaricatis 2–3.5 cm. longis, 1.5–2 mm. latis, seminibus oblongis immarginatis 2–2.5 mm. longis, ca. 1.5 mm. latis, cotyledonibus accumbentibus.

Holotype in the Gray Herbarium, collected in an open seepage area below timberline on a steep and rocky, west-facing, serpentine slope, upper end of Rattlesnake Meadows, Preston Peak, 41°49.8′ N. latitude, 123°38′ W. longitude, Siskiyou County, California, June 26, 1972, *Chester A. Ground and Gilbert J. Muth 1790.*

Perennial, glabrous throughout; stems simple, one from each single rosette or a few from several rosettes on a branching caudex, erect, 1.5–3 dm. high; basal leaves in a dense flat rosette, short petiolate, broadly obovate, rounded distally, entire to remotely and shallowly dentate, thickish, 1.5–2.5 cm. long, 1–1.5 cm. wide; cauline leaves 2–5, sessile, not auriculate, remote, 3–6 mm. long, 2–3 mm. wide; inflorescences racemose, elongating in fruit; sepals dark purple, erect, oblong, 4.5–5.5 mm. long, outer pair saccate, inner pair plain; petals spatulate, not differentiated into blade and claw, light purple to lavender, 12–15 mm. long, 3–5 mm. wide; stamens erect, strongly tetradynamous; filaments purplish above; anthers ca. 1 mm. long; fruiting pedicels divaricate, 4–8 mm. long, decreasing in length from base to apex of infructescence;

siliques divaricate to divaricately ascending, strongly single-nerved from base to apex, 2–3.5 cm. long, 1.5–2 mm. wide, sessile or with a very short gynophore; styles 0.5 mm. to obsolete; seeds in a single row, wingless, oblong, brown, 2–2.5 mm. long, ca. 1.5 mm. wide; cotyledons accumbent.

Additional specimens studied, all from the same general locality as the holotype. Dry serpentine ridge, 5,800 ft., July 31, 1971, *Ground* 888 (GH); same population as holotype, Aug. 2, 1972, *Ground & Muth 1794* (GH); 6,000 ft. Aug. 2, 1972, *Ground & Muth 1795* (GH).

The significant differences between *Arabis serpentinicola* and *A. aculeolata* involve the seeds, the presence or absence of trichomes and the length or absence of a style on the fruit. *Arabis serpentinicola* is wholly glabrous while *A. aculeolata* is always hirsute. The portion of the seeds occupied by the embryo is somewhat similar in the two species but there is a pronounced distal wing and minor wing-margins on the sides of the seeds of *A. aculeolata* whereas the seeds of *A. serpentinicola* are wingless. In some siliques of the latter species, there is a very short rather stout style about 0.5 mm. or less long but in others the stigma is virtually sessile. On the other hand, the siliques of *A. aculeolata* have a slender style 1.5–2 mm. long. Another difference that appears to have some value for distinguishing these species is the shape of the silique apex, being accuminate in *A. aculeolata* and blunt in *A. serpentinicola*.

There is no doubt about the close relationship of these two species which are similar in habit, the nature of the basal and cauline leaves and the flowers. On the whole, *Arabis aculeolata* has longer siliques and pedicels than those of *A. serpentinicola*, and the siliques tend to be more erect. The flowering and fruiting period does not coincide in the two species. *Arabis aculeolata* begins flowering in March in some years but is usually at its flowering peak in April or May. In June and July, *A. serpentinicola* reaches its flowering maximum. Part of this difference may be associated with the differences in altitude where the two species grow. *Arabis aculeolata* is found mostly below 2,000 ft. while *A. serpentinicola* occurs above 5,000 ft.

2. **Arabis aculeolata** Greene

Although we have seen in excess of twenty different collections of this species, it is not certainly known outside of Josephine County, Oregon. There is a single collection at the California Academy of Sciences made by Alice Eastwood in extreme northern Del Norte County, California, and referred by her to *A. mcdonaldiana*, which I have tentatively placed in *A. aculeolata*. The material is in flower only and is hard to deal with on that account. However, it clearly is not *A. mcdonaldiana*. The specimens are small for *A. aculeolata* and the trichomes are less ascicular than in typical specimens but otherwise they seem to fall within the range of variation of that species.

Most of the specimens available for study are in flower because the plants are most conspicuous at that stage and collectors are attracted to

them. Of the six collections with reasonably mature siliques, all but two have sessile siliques. In one collection, *Constance and Rollins 2967* (DS,GH), some plants have shortly stipitate siliques while in others the siliques are sessile. In one collection, *Eastwood and Howell 1424* (CAS), the siliques are uniformly stipitate and the stipe is ca. 2 mm. long. Such a character, although sometimes variable within a species, usually does not range as widely as in this case. Flower size is variable as indicated by the specimens examined, also considerable variation in the height of the plants is evident. Looking at the species as a whole, there is an uncommon amount of variation present even though the total geographic range is relatively limited. This may be explained by the probability that the serpentine areas where *A. aculeolata* grows are somewhat separated and the individual populations have evolved in slightly different directions. From such evidence as we can see and measure from the specimens alone, this species would appear to be a good subject for the detailed study of population variation and population disparity within a single species.

3. **Arabis mcdonaldiana** Eastwood

There are only three collections of this species known to me, two more than I had to work with in 1940. All three are from the same place, summit of (Big) Red Mountain, northern Mendocino County, California. Both the type series, *Eastwood* in 1902 (CAS,GH), and *Constance and Rollins 3002* (DS,GH) are mostly in flower with, at most, immature siliques. Fortunately a newer collection, *Gankin, Hildreth, N. and I. Knight 2722* (CAS), has mature fruits. Thus, for the first time it has been possible to determine that the siliques are accuminate at apex and tipped with a style about 1 mm. long. The seeds are oblong, about 2 mm. long, 1–1.2 mm. wide, with a definite distal wing and narrow or nearly obsolete wing-margins along the sides. A distinctive feature of *A. mcdonaldiana* is the short few-fruited infructescence. Only 2 to 4 siliques mature near the apex of the slender stems.

4. **Arabis oregana** Rollins

Although there are a number of newer collections available since my treatment of this species in 1941, they do not provide much additional information. However, it is clear that *Arabis oregana* is not a serpentine inhabiting species. At two stations about three miles apart where Dr. Constance and I found it growing with *Holodiscus, Cercocarpus* and *Ceanothus*, south of Ashland, Oregon, the plants were in a rich deep soil and there was no evidence of serpentine rocks in the vicinity. Most of the known collections are from Jackson County, Oregon, but we found the species near Scott River, 10 miles southwest of Scott Bar, Siskiyou County, California. The specimens of this collection are unusual in being nearly glabrous but are otherwise similar in most respects to the Oregon

material. The California collection, *Constance and Rollins 2915* (DS,GH), has the characteristic trichomes of *A. oregana* on the margins of the basal leaves which along with the general features of the plants point to their identity with that species.

5. **Arabis modesta** Rollins

At the time *Arabis modesta* was described, mature fruiting material was not available. Now with ten new collections for study, we still have only two with mature fruits and seeds. In one of these, *Ripley and Barneby 9622* (CAS), from Rogue River Canyon, 5 miles above Galice, Josephine County, Oregon, both pedicels and siliques are divaricately ascending and the siliques are accuminate at the apex. The style is slender, 1.5–2 mm. long. The seeds are oblong, ca. 2 mm. long, slightly wider than 1 mm., and are very dark, the distal wing being nearly black. The other collections, *Harris 21397* (GH), from near the mouth of Scott River, Siskiyou County, California, is similar in most respects but the styles are less than 0.5 mm. long and the siliques are straighter than in the Oregon specimens.

In some of the new collections, the specimens are up to 6 dm. tall which is about 1.5 dm. more than we had seen previously. However, the most notable collections are those of *Donald V. Hemphill* (CAS,GH) from near Monticello Dam, Napa-Yolo county line, California. These specimens not only represent a considerable southward extension of the species range but they also show minor differences when compared to those of the California Siskiyou region or of southern Oregon.

Arabis modesta overlaps the range of *A. oregana* in northern California and southern Oregon and there is one collection, *Applegate 4598* (DS), from about 10 miles southeast of Ashland, Oregon, that suggests the possibility of hybridization between these species. The specimens are nearest to *A. modesta* but the trichomes are slightly larger than in unadulterated plants of the species, and the lower stems and basal portions of the petioles have simple trichomes present to a limited degree. The trends toward larger trichomes and toward simple trichomes are in the direction of *A. oregana*.

6. **Arabis blepharophylla** Hooker & Arnott

There is considerable variation in the coarseness of the pubescence on different plants of *Arabis blepharophylla* both within populations and between populations. In the most extreme forms in one direction, represented by the collections from Bodega Bay in Sonoma County, California, for example, the pubescence is quite uniform on leaves and stems. The trichomes are small, dendritically branched with mostly four prongs, and the leaves show no suggestion of being ciliate-margined. In another direction, exemplified by the type of the species and other specimens from the Presidio area of San Francisco, the trichomes are much coarser and usually

three or two pronged but often with unbranched ones mixed with them. Furthermore, the leaves are most often ciliate and the lower portions of the stems usually possess spreading trichomes.

Other types of variations include the length of the siliques and whether they are blunt or somewhat tapered at apex, the length and thickness of the styles and the height of the plants. However, in spite of the rather considerable evident variation, this species hangs together quite well and I cannot distinguish any infraspecific taxa. Characters that appear to be distinctive turn out to be uncorrelated with other characters that might otherwise be utilized to set off distinctive taxa.

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A RECONSIDERATION OF THELYPODIUM JAEGERI

REED C. ROLLINS

The need for a reevaluation of the generic lines in the *Thelypodium* complex of the Cruciferae has been recognized for some time (Rollins 1941, 1957). In the last several years one of my graduate students, Dr. Ihsan Al-Shehbaz, has been studying this problem as part of his thesis research (1973). From a very exhaustive assembling of evidence and the careful evaluation of it, he has concluded that *Thelypodium* should be interpreted as being less inclusive than it is given in some of the current floras. Although it differs in many respects, his treatment of *Thelypodium* comes fairly close to that of Payson (1923) as far as its general interpretation of generic limits is concerned. My own assessment of the species to be included in *Thelypodium* coincides in a general way with the findings of Payson and of Al-Shehbaz. Under such an interpretation, one of the species I described in *Thelypodium*, *T. jaegeri*, has to be excluded. This ultimate exclusion of *T. jaegeri* from *Thelypodium* was actually anticipated at the time the species was described.

As a general principle, the classification of a group of organisms is best portrayed if related species are properly aggregated into genera even if some species are more remote in their relationship than others to the biologically central core of species of the genus. Monotypic genera should be avoided whenever possible because they leave the included species without a formally indicated close relationship position within a taxonomic framework. However, there are cases where species simply do not fit into established genera and it is not possible to say what their closest relatives might be. The position of *Thelypodium jaegeri* is a case in point. This species does not fit with those of an established genus of the Cruciferae. For this reason, we have concluded that an independent genus must be established to receive it. Fortunately, there is now enough material to provide the basis for a reasonably adequate study of *T. jaegeri*. This was not the case when the species was first described in 1941.

Caulostramina Gen. Nov.

Herba glabra caespitosa multicaulis, caulibus gyrosis simplicibus vel rare superne ramosis, foliis petiolatis, inflorescentiis racemosis, sepalis purpureis oblongis non saccatis, petalis purpureis spathulatis, infructescentibus laxis, siliquis linearibus; seminibus oblongis, immarginatis, cotyledonibus incumbentibus.

Type species: *Caulostramina jaegeri* based on *Thelypodium jaegeri* Rollins. The generic name is suggested by the fact that the older persistent stems become straw-colored.

Caulostramina jaegeri (Rollins) comb. nov.

Thelypodium jaegeri Rollins, Contrib. Dudley Herb. 3:174. 1941. Holotype: shaded rock crevices, "Teufel" Canyon, southern end of Inyo Mts., about 25 miles north of

Darwin, Inyo Co., California, May 31, 1940, *E. C. Jaeger s.n.* (GH); isotypes: DS,POM.

The additional collections of this species we have studied are given below. These provide extensive material but none of the specimens possess fully matured seeds. All are from Inyo County, California, and the localities so far known show that the species is very restricted in its total distribution. Inyo Mountains: The Narrows, head of Marble Canyon, Sept. 19, 1954, *P. A. Munz and J. C. Roos 20175* (CAS,RSA); same location, June 29, 1954, *J. & L. Roos 6185* (RSA,UC); Marble Canyon, July 11, 1941, *Annie M. Alexander and Louise Kellogg 2528* (CAS,DS,GH,POM,UC,US,UTC,WSC,WTU); Teufel Canyon May 20, 1938, *E. C. Jaeger s.n.* (GH,POM); Teufel Canyon, about 17 miles north of Darwin, May 31, 1940, *E. C. Jaeger s.n.* (DS,GH,NY,RSA); just below summit of Cerro Gordo Peak, June 27, 1942, *Alexander and Kellogg 3033* (CAS,COLO,DS,GH,NY,RSA,RM,UC, US,UTC,WSC,WTU); north slope of Cerro Gordo Peak, east of divide, July 4, 1942, *Alexander and Kellogg 3033a* (CAS,DS,F,GH,MO,NA,NY,POM,PM,UC,UTC,WSC,WTU).

There is some variation in leaf shape and leaf margin in *Caulostramina jaegeri* but all of the leaves are basically of the same pattern. Young seedlings grown at the Rancho Santa Ana Botanic Garden show even the earliest leaves to be long petioled. The petiole is relatively slender, broadening gradually only slightly then flaring abruptly into the broad nearly orbicular blade. Internodes develop between the early formed leaves so that a basal cluster or rosette of leaves with shortened internodes is not formed as in many genera of the Cruciferae. In this respect, the plants are somewhat like the genus *Stanleya* or the genus *Chlorocrambe*.

Mature leaves occurring at relatively long intervals on the active stems are slender petioled. The blades vary from broader than long, when they tend to be slightly cordate, to longer than broad when they are broadly cuneate toward the petiole junction. The blade margin may be entire to slightly undulate or with broad and blunt teeth. The leaves are bluish green which is characteristic of many arid area crucifers.

An outstanding feature of *Caulostramina jaegeri* is the caespitose habit with the numerous stiffish, almost wiry stems intermeshed in a thick cluster on the upper portion of a heavy root-stalk. The stems are mostly unbranched and are gyrate at least in the lower portion. They are very persistent, the lower portions forming a dense covering over the elongated root-stalk. The older stems become straw-colored and are eventually broken off leaving the lower portion as a part of a thick thatch that makes up the basal part of the plant.

Some collectors describe the petals of *Caulostramina jaegeri* as being white, drying lavender, while others say "flowers lavender." Mr. E. C. Jaeger, the discoverer of the species noted, "Flower color and veining as in *Raphanus*." In the dried specimens, the lavender color predominates. It is possible that two color forms occur under natural growing conditions. Although the siliques are nearly straight to slightly curved in the immature state, they are somewhat arcuate on some specimens where they are nearly mature. In my original description, I had indicated the siliques to be "straight or nearly so" but that observation was made on specimens with immature fruits. A photograph of a plant growing at the Narrows in

Marble Canyon, kindly provided by Mary DeDecker of Independence, California, shows the siliques diverging from the rachis of the infructescence at a very wide angle. These fruits are approaching maturity but instead of being arcuate, they are irregularly curved or bent back and forth in an undulating fashion.

Caulostramina jaegeri grows in limestone crevices, usually on north-facing slopes or cliffs. Its habitat is assumed to be an ancient one from the point of view of potential plant habitation because it is an area where Bristle Cone Pine, one of the oldest, if not the oldest, known living plant species occurs.

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SYSTEMATICS AND EVOLUTION OF THE GENUS CAKILE (CRUCIFERAE)

JAMES E. RODMAN[1]

INTRODUCTION

On November 14th, 1963, a submarine volcano erupted in the North Atlantic 20 miles south of Iceland and eventually created the new island of Surtsey. Access to the island was restricted by the Icelandic government in the interests of scientifically monitoring its developing biota. In June, 1965 the first vascular plants growing on Surtsey were discovered—seedlings of the sea rocket, *Cakile*. In the summer of 1967 plants of *Cakile* were found in flower and fruit, and along with lyme grass (*Elymus arenarius*) and angelica (*Angelica archangelica*) these initiated the primary colonization of Surtsey by the higher plants (Thorarinsson 1967).

The Surtsey event epitomizes two of the salient characteristics of the biology of sea rockets: dispersal and colonization. It was certainly not an isolated incident although it is rare to find such a well-documented one. In the western Caribbean, for example, Stoddart (1963, 1969) described the colonization by *Cakile lanceolata* of sand cays off Honduras following their devastation by Hurricane Hattie. Several authors (Davis 1942; Heslop-Harrison 1954; Hewett 1970) have noted the fluctuating appearance and disappearance of sea rockets locally along a coast. The dynamic nature of dispersal in the genus is even more evident in accounts of its accidental dispersals by man, resulting in tremendous extensions of the distributional range of some species. *Cakile edentula* and *C. maritima,* for example, have been introduced to, and become naturalized throughout, the Pacific Coast of North America (Barbour & Rodman 1970) and temperate coastal Australia (Sauer 1965; Sims 1968). The Old World *C. maritima* has been collected on ballast ground near ports on the Atlantic and Gulf coast of North America, in Argentina and Uruguay, and even in New Caledonia.

The result of these migrations, historically recent and geologically old, has been the creation of a confusing array of sympatric forms throughout much of the range of the genus. Particularly in the New World, two or more taxa of *Cakile* are now known from every major area of its distribution. Combined with a lack of systematic investigations based on field studies, this situation has led to confusion in the taxonomy of the sea rockets which recent work has not dispelled. In turn, this has limited the comprehension of evolutionary patterns and relationships in the genus and led occasionally to facile conclusions concerning general biological phenomena.

A recent monograph of the genus (Pobedimova 1963, 1964) appeared

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concurrently with a treatment of the European sea rockets resulting from work on the Flora Europaea project (Ball 1964a,b); they offer quite different interpretations of the taxonomy of Old World *Cakile*. Moreover, a number of authors have expressed dissatisfaction with the treatment of the American taxa (Rollins 1966; Taylor & Mulligan 1968). Omission of validly published names, incorrect citation of types, failure to designate lectotypes, among other shortcomings, apply to the latest treatments. This study was undertaken to provide a more critical taxonomy of *Cakile* as a basis for the investigation of those aspects of its biology of more general interest such as dispersal, hybridization, and speciation.

Data included here derive from more than 100 field collections and from approximately 3700 herbarium collections assembled from 41 institutions. In addition to morphological studies, particularly on the flowers, fruits and seeds, chemical analyses of the seeds for mustard oil glucosides (glucosinolates) by paper and gas chromatography were conducted on approximately 100 field or greenhouse collections as well as seed samples sent from Australia, Iceland, Norway, and Denmark. This chemosystematic investigation, and that of Dr. Ihsan Al-Shehbaz done on the genus *Thelypodium*, constitutes the first extensive survey of these secondary plant products for monographic purposes. Forty-seven collections, representing most of the taxa in the genus, were grown in environmental chambers to assess genotypic differences under uniform conditions. In conjunction with this, observations were made on seed germination, seedling growth, and photoperiodism. Aspects of the breeding systems of *Cakile* were studied: self-compatibility, floral phenology, and spontaneous fruit set. A limited number of artificial hybridizations were made, and the resulting F_1 plants were grown to maturity and tested for pollen viability and fertility. An interest in the dispersal ecology of these plants led to experiments on the duration of time the fruits can float in sea water and on the effects on seed germination. Preliminary counts of chromosomes and a review of the literature suggested that cytological analyses would not be of taxonomic value within the genus; consequently, no extensive chromosome study was made.

The combined data from a study of the morphology, glucosinolate chemistry, breeding systems, and genecology of *Cakile* have been utilized to construct a classification of the taxa and a probable phylogeny. Then, an interpretation of the geographical distribution of the genus through geological time is offered. While this classification purports to be phenetic, acquaintance with modern evolutionary theory has influenced my interpretations of the observed patterns. A rigorous numerical analysis of the data would be valuable but was not undertaken.

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Taxonomic History

The history of the taxonomy of *Cakile* may be divided into three overlapping phases corresponding to three major intellectual concerns of the times. The first period, rooted in the pre-Linnean works of Tournefort and the early herbalists, spanned the years from Linnaeus' "Species Plantarum" to the great "Prodromus" of De Candolle and witnessed the development of a generic concept or circumscription regarded as "natural," that is, based on several characters of different parts of the plant. The principal features of this period of botanical ferment—the increasing precision in terminology accompanied by a quest for new characters, the standardization of nomenclatural procedures, the slow progress of empirical, inductive classification over essentialist systematizing (Stafleu 1971)—can be illustrated by the systematic treatment of *Cakile* at that time. From an array of names and descriptions published under the genera *Cakile*, *Bunias*, *Isatis*, *Rapistrum*, and *Raphanus* there emerged a generic concept based principally on the indehiscent, two-jointed, corky fruit with accumbent seeds, the fleshy, glabrous leaves and stems, and a vague association with a particular habitat, the maritime strand. This concept was in a sense codified in the "Systema Naturale" and "Prodromus" of A. P. De Candolle, and the subsequent taxonomic history of the sea rockets remains remarkably free of the generic vicissitudes which have plagued so many groups of Cruciferae. The second phase, from the time of De Candolle long into the present century, reflects considerable taxonomic activity of a typological nature. The methodology was the same as that of Linnaeus and many of his contemporaries, but it was applied to the recognition of species and especially of infraspecific taxa, well over 50 names in infraspecific categories being published. Characteristically, taxa were described on the basis of differences in fruit or leaf morphology uncorrelated with other characters and with little or no attention directed to the nature and extent of variation in populations (cf. Schulz 1903 especially). Indeed, it is a concern with population variation and character correlations as well as with such larger questions as evolutionary origins and phylogeny which permeates, to widely varying degrees, the modern work of the third phase, found principally in the publications of Ball (1964a,b) and Pobedimova (1963, 1964).

The nomenclatural history of *Cakile* begins in 1753 with the "Species Plantarum" in which Linnaeus classified Old and New World sea rockets (having seen specimens from both hemispheres) as the species *Bunias Cakile*. The plants bear only a superficial resemblance to *Bunias*, and Linnaeus' treatment reveals his limited knowledge of the indehiscent-fruited, nucamentaceous Cruciferae. A distinct generic concept antedated Linnaeus' rather novel idea; he acknowledged this by using Tournefort's generic name, *Cakile*, as the epithet in his new binomial.[2] His concept of the plants was apparently not well-defined, however, since he also described a specimen of *Cakile maritima* under the name *Isatis aegyptica* in "Species Plantarum." The diagnosis is inadequate for resolving the issue, and unfortunately no specimens exist in the Linnean Herbarium, a situation early noted by Willdenow (1800; cf. Savage 1945). The association of this name with the genus *Cakile* was, however, made by Linnaeus' contemporaries and immediate followers and by a number of later taxonomists. In the herbarium of Linnaeus' student Pehr Forskål in Copenhagen are sheets of *C. maritima* (seen on microfiche) marked "Isatis aegyptiaca F."; these presumably constitute the basis for the record of *Isatis aegyptia* (note the variant orthography) in Forskål's "Flora Aegyptiaco-arabica." Forskål at least was more consistent than his teacher in his classification of sea rockets; specimens with pinnatifid leaves were described by him, not in *Bunias*, but as *Isatis pinnata*.

In accord with the rules of the International Code of Botanical Nomenclature, the genus *Cakile* was first described by Philip Miller in the 1754 edition of "The Gardeners Dictionary . . . Abridged" in which he did not employ Linnean binomials (Dandy 1967). Scopoli, in the 1772 edition of his "Flora Carniolica," where he adopted the Linnean system of binomials, provided a new name, *Cakile maritima*, for *Bunias Cakile* L., to avoid coining a tautonym. *Cakile maritima* Scop. thus constitutes the type species of the genus. Prior to Scopoli's name, Crantz had published the combination *Rapistrum cakile* (L.), but this generic association was accepted only by Bergeret who then effected the superfluous combination *Rapistrum maritimum* (Scop.). The lack of consensus on a generic circumscription is further illustrated in Willdenow's "Species Plantarum" where he published *Cakile aegyptiaca* and *Raphanus lanceolatus*, the latter described from a specimen collected in "Antillis." The identity of this species as a *Cakile* was not established until 1903, and for nearly a century the sea rockets of the West Indies were known by the name *C. aequalis*. In 1814, in his "Florula Bostoniensis," the Boston physician Jacob Bigelow described *Bunias edentula* from plants collected on the sandy

[2] The name *Cakile* is a Latinization of an Arabic term [transliterated "qaqulleh" (Black 1924) or "qaqoulla" (Cosson 1887)] used by Serapion the Younger, an 11th–12th century Arab physician whose popular manuscript on medicinal plants and simples, "De simplici medicinae," had been translated in the 13th century and was first printed in 1473 (Stillwell 1970). Joseph Gaertner commemorated him with the name *Cakile serapionis*.

beaches of Cape Ann and South Boston. Four years later Thomas Nuttall, more aware of the progress in European taxonomy but apparently unacquainted with that in his adopted country, described the same species as *Cakile americana*. Linnaeus' ideas must still have been fresh, however, for in so doing, Nuttall (1818) wrote: "in fruit this species approaches *Bunias*, and seems to evince the property of again uniting these 2 genera."

The confusion of generic concepts ended with A. P. De Candolle. In his treatment of *Cakile* in the "Systema Naturale" and the "Prodromus" he synthesized the results of several developing lines of research on the fruits and seeds of Cruciferae and assembled a suite of reproductive and vegetative features characterizing plants associated with a particular habitat, the coastal strand. This habitat was virtually a generic character until 1911 when *C. arabica* from the Nefud Desert was described by Velenovsky and Bornmüller. The taxonomic work on sea rockets subsequent to De Candolle's synthesis has accepted implicitly the "natural" character of his circumscription of the genus.

For the remainder of the 19th century taxonomic work on *Cakile* consisted largely of the description of infraspecific taxa of *C. maritima* by both Old and New World systematists. One noteworthy study of intraspecific variation in this species, though ultimately of little taxonomic value, was made by Jordan (1864) in his pioneering genecological investigations. In 1900 the American taxonomist C. F. Millspaugh, following his collecting trip through the West Indies, monographed the genus. Millspaugh's recognition of eight species in the New World reversed a long tradition maintained by 19th century North American botanists who had treated the American sea rockets as varieties of *C. maritima*. Undoubtedly, Millspaugh's field experience strongly influenced his decision to emphasize at species rank the differences between the American plants. Three years later a second monograph of *Cakile* appeared in Urban's "Symbolae Antillanae," prepared by O. E. Schulz in Berlin. Schulz accommodated the eight species recognized by Millspaugh along with several newly described taxa within an extensive hierarchy of infraspecific categories of a single American species of sea rocket, *C. lanceolata*. His curious treatment provoked from N. L. Britton (1906) the comment: ". . . the attempt of Mr. Schultz [sic] to classify the plants of this genus into named forms and varieties of various ranks serves no useful purpose whatever, and does not express their real relationships at all; the only advance that he has made in their study is to point out an older name for the species long known as *C. aequalis* L'Hér." In 1923 Schulz published a treatment of *Cakile* for "Das Pflanzenreich" in which he recognized two American species, *C. edentula* and *C. lanceolata*, within his "species collectiva," *C. lanceolata*. Basically this treatment duplicated his earlier one with only changes in rank being made. The judgment of his peers remained much the same; Ball (1964a), for example, remarked

that "Schulz's account of the variation within *C. maritima* and *C. edentula* was not very satisfactory and has not been generally accepted." Schulz's work epitomizes a taxonomy almost completely divorced from considerations of the biological meaning of character variation. In methodology it reduces itself virtually to the nomenclatural recognition of individual herbarium specimens.

The third and latest monograph of the genus, in which 15 species are recognized, was prepared by E. G. Pobedimova (1963, 1964) in Leningrad. It appeared concurrently with the treatment of the European sea rockets by P. W. Ball (1964a,b) for the Flora Europaea project. The two offer rather different interpretations of the variation in European *Cakile* although both share a common philosophical approach to taxonomy, viz. that taxa are recognized on the basis of character correlations and possess a particular geographic range. Their differences stem in part from differences in the herbarium collections utilized by each, but largely from a difference of opinion concerning the rank at which taxa should be treated, with Pobedimova adopting a very narrow view of species. In her treatment of the New World sea rockets Pobedimova virtually duplicates that of Millspaugh in his 1900 monograph; this approach may have been conditioned by the fact that she studied specimens from only three American herbaria (DAO, UBC, US). Consequently she contributes little to an understanding of the bewildering array of forms on the shores of the Caribbean and Gulf of Mexico. In addition to the classification, Pobedimova offered a phylogeny of the species, admittedly speculative, along with an extensive discussion of the geological setting for the evolution of the species of *Cakile*. Dissatisfaction with this latest treatment has been expressed by a number of workers (Rollins 1966; Taylor & Mulligan 1968) and seemed to invite yet another attempt to elucidate relationships in this genus.

Generic Affinities

The generic affinities of *Cakile*, as suggested in the several systems of Cruciferae proposed since the time of De Candolle, are presented in Table 1. In general, *Cakile* has been associated with genera of the tribe Brassiceae *sensu* Schulz (1936) on the basis of fruit and nectary morphology. Only Prantl's (1891) system deviates significantly from this pattern, and his curious juxtaposition of such disparate genera as *Sisymbrium* and *Cakile* has understandably attracted few supporters. The alliance of *Cakile* with genera of the Brassiceae is clear; its position within the tribe, whether a basal, primitive stock, intermediate, or an advanced end-point of evolution, is much less clear.

Pobedimova (1963) considered *Cakile* to be derived from *Erucaria* by reduction in the number of seeds per fruit segment, loss of pubescence (she was unaware of the pubescence in *C. arabica*), and change to ac-

cumbent seeds. The inland "sea rocket," *C. arabica*, appears, in habitat and pubescence, to be a link between the strand species of *Cakile* and *Erucaria*, a genus of desert annuals of the Mediterranean region. In what

TABLE 1. GENERA ASSOCIATED WITH CAKILE IN THE SYSTEMS OF CRUCIFERAE

Author	Date	Tribe	Genera	
De Candolle	1821	Cakilineae	Chorispora Cordylocarpus	Rapistrum
De Candolle	1824	Cakilineae	Chorispora	Cordylocarpus
Bentham & Hooker	1862	Cakilineae	Crambe Enarthrocarpus Erucaria Fortuynia Guiraoa	Hemicrambe Morisia Muricaria Physorhynchus Rapistrum
Wettstein	1889	Cakilineae	Chorispora Cordylocarpus Crambe Didesmus	Enarthrocarpus Erucaria Rapistrum
Prantl	1891	Sinapeae, subtribe Sisymbriinae	Ammosperma Andreoskia Boreava Calepina Chartoloma Erucaria Goldbachia Isatis	Myagrum Pachypterygium Sameraria Schimpera Sisymbrium Spirorhynchus Tauscheria Texiera
Bayer	1905	Brassiceae	Brassica Crambe Diplotaxis Eruca Erucaria	Erucastrum Moricandia Raphanus Rapistrum Sinapis
Hayek	1911	Brassiceae, subtribe Raphaninae	Calepina Ceratocnemum Cordylocarpus Cossonia Crambe Enarthrocarpus Erucaria Fortuynia Guiraoa	Hemicrambe Kremeria Morisia Otocarpus Physorhynchus Raphanus Rapistrum Reboudia Zilla
Villani	1926	Sinapeae	Cordylocarpus Crambe Didesmus Enarthrocarpus Erucaria Fortuynia Guiraoa Hemicrambe	Hirschfeldia Morisia Muricaria Otocarpus Physorhynchus Rapistrum Reboudia Sinapis
Schulz	1923, 1936	Brassiceae, subtribe Cakilinae	Erucaria	
Janchen	1942	Brassiceae, subtribe Cakilinae	Erucaria	

is probably the most extensive discussion of evolution within the tribe Brassiceae, Rytz (1936) also argued that *Cakile* had evolved from *Erucaria* but, in addition, *Cakile* represents the basal stock for a group of genera constituting his subtribe Rapistrinae (*Calepina, Ceratocnemum, Crambe, Didesmus, Kremeria, Muricaria, Rapistrum*). Rytz's views focused primarily on aspects of fruit morphology. In the Brassiceae he distinguished between "valvar" and "stylar" or "beak" portions of the mature fruit and postulated an evolutionary trend toward reduction of the valvar portion (reduction in size and in number of ovules and seeds), primary increase in the stylar portion or its elaboration into an appendage, and secondary reduction of the stylar portion of the fruit. He considered *Cakile* an intermediate in the reduction series from *Erucaria* leading to such presumably recent products of evolution as *Crambe, Calepina,* and *Kremeria.* These trends in fruit morphology appear to be valid, but the neat linear series which Rytz proposed for the evolution of the genera undoubtedly oversimplify a more reticulate pattern of relationships. Specifically, the series from *Erucaria* through *Cakile* to *Rapistrum* would involve a change in cotyledon position from conduplicate to accumbent back to conduplicate (Zohary 1966) and a change in ovular position along the replum from alternating on both sides to restricted to one side back to alternate (Schulz 1936). It appears simplest to postulate a parallel series of reductions, with *Cakile* the end-point of one of these lines of evolution. An ultimate rather than intermediate status seems more consonant with the nearly unique strand habitat of *Cakile* (excepting *C. arabica*), otherwise rare in the Cruciferae.

Morphology and Anatomy

Habit. All the species of *Cakile* are succulent, branched, erect to prostrate, herbaceous plants. In favorable sites, large plants may develop a woody caudex, becoming suffrutescent. Plants rarely exceed a meter in height and vary from a few decimeters to 1.5 m in diameter. A collection of *C. lanceolata* ssp. *lanceolata* from Jamaica (*Harris 11628,* GH) bears the note: "plant up to 5 feet high," though whether erect or, more likely, sprawling over other plants is not indicated. A collection of *C. lanceolata* ssp. *fusiformis* from Dade County, Florida (*Gillis 7659,* GH), bears the observation: "plants up to 2 m long." In both cases, it is probably the length of fruiting racemes which was estimated.

The erect habit is generally encountered in *Cakile edentula* in its native range and in *C. geniculata* while *C. maritima, C. constricta,* and *C. lanceolata* vary from erect to more commonly prostrate and sprawling. Numerous collections of *C. edentula* from Australia, where it is naturalized, indicate that the plants are often prostrate, a habit occurring only rarely in the species' native range and along the Pacific Coast of North America where it is also naturalized. I have not seen *C. arabica* or *C.*

arctica in the wild but to judge from herbarium collections, the former commonly has an erect habit and the latter varies from erect to often prostrate. In the species with an erect growth habit, the branches (which arise near the base in all species) curve outward and upward. The plants often become quite compact and if uprooted when dead and dry may be blown along the beach like tumbleweeds (Cowles 1899). Branches in the more prostrate species vary from procumbent to decumbent.

Root. Sea rockets develop a stout taproot, rarely exceeding 4 dm in length and 2 cm in diameter, along with several long, thin horizontal roots. The latter may extend over 15 dm (a specimen of *Cakile geniculata*, *Thieret* 25753, GH) and usually grow only a few centimeters below the surface. These probably function quite efficiently in anchoring the plants in the sand. They may also be adapted to absorbing the water which results from "internal dew formation" in dune sands (Salisbury 1952; Chapman 1964).

Stem. The stems of sea rockets are succulent to varying degrees, curved, sinuous, or flexuous, smooth or weakly striate, and terete in cross-section. They are commonly green, becoming tan with age, but occasionally developing a purple coloration especially at the nodes. The stem possesses a thick epidermis with outer cell walls 10 μ thick in *Cakile edentula* (Starr 1912) and *C. maritima* (Wright 1927). The epidermal cells are heterogeneous in size as in the leaf. In *C. maritima*, long tubular myrosin cells occur primarily in the outer cortex but are also found sporadically in the pith near vascular bundles (Wright 1927).

Leaf. The cotyledons and true leaves of sea rockets are characteristically succulent, a feature widely interpreted as an adaptation for water storage. The degree of succulence varies between taxa but is of little diagnostic value, especially in pressed herbarium specimens. In the American taxa studied in the field, I found the leaves of *Cakile lanceolata* to be less succulent than those of *C. edentula* and *C. geniculata*, with *C. constricta* intermediate. A collection of *C. geniculata* (*Thieret* 29350, A) bears the note: "leaves about 1.5 mm thick." Chrysler (1904) reported the thickness of leaves of sea rockets collected at Woods Hole, Massachusetts (undoubtedly *C. edentula* var. *edentula*), as 1.17 mm and plants from Chicago (probably *C. edentula* var. *lacustris*) as 0.76 mm. He stated that less succulent leaves were characteristic of lacustrine plants compared to their maritime relatives, which appears to be true in *Cakile*.

Leaf morphology varies from broadly ovate with ± entire margins to deeply pinnatifid. Leaf shape distinguishes some taxa but varies in others. In *Cakile arabica*, the leaves are finely pinnatifid, with lobes and rachis rarely exceeding 2 mm in width and with the lobes widely separated and themselves occasionally lobed. Deeply pinnatifid to entire leaves occur in *C. maritima* and *C. lanceolata* ssp. *fusiformis*. In all the species, leaves formed late in the season are usually much smaller and less dissected than

the early leaves. Occasionally one of these small leaves subtends the first flower and fruit of the raceme, which is otherwise ebracteate.

Leaf anatomy has been investigated by a number of workers (Chrysler 1904; Harshberger 1908 & 1909; Starr 1912; Wright 1927). The summary presented here is supplemented by my own observations on leaf material of *Cakile edentula* var. *edentula* collected near Boston, paraffin-embedded, and stained with safranin-fast green. The leaf epidermis is thinly cutinized, and its cells are heterogeneous, a few being much larger than the rest. Stomates, more numerous abaxially, are of the typical cruciferous type and are flush with the surface in *C. maritima* (Wright 1927) and in *C. edentula* (Harshberger 1909, as "C. maritima") but partly sunken in *C. lanceolata* (Harshberger 1908, as "C. aequalis"). The leaf parenchyma is not clearly differentiated into distinct palisade and spongy mesophyll. Wright (1927) stated that the mesophyll is undifferentiated in *C. maritima,* with the outer layers simply possessing more intercellular spaces. Harshberger (1908) and Starr (1912), however, described a palisade layer of vertical cells on both sides of the leaf (a "diplophyll") with a central spongy mesophyll of more compact cells in American taxa. Metcalfe and Chalk (1950) repeated this distinction, but the differences may well be artifacts of limited sampling. Myrosin cells, elongated and tubular, were observed throughout the leaf of *C. maritima,* following staining with Millon's reagent or orcin and HC1 (Wright 1927). I observed darkly green-staining cells, irregular in shape, scattered throughout the leaf of *C. edentula;* these are probably the myrosin cells although safranin-fast green is not a differential stain for these. Schweidler (1905) placed *Cakile* in his class "Exo-Idioblastae," as possessing idioblasts (myrosin cells) in the leaf mesophyll but not in the vascular bundles. Wright (1927) found that myrosin cells occur throughout vegetative and floral structures of *C. maritima,* including the vascular system of the root, and concluded that the genus more appropriately belonged in Schweidler's class, "Hetero-Idioblastae," although Schweidler had based his classes on the presence of myrosin cells in leaf tissue alone. Hydathodes are usually present at the end of the leaf, terminating the three major vascular strands; in young leaves they are often purplish.

The succulent cotyledons of sea rockets are commonly oblate-lanceolate, about 2–4 cm long, and ± equal in length. Lubbock (1892) stated that the cotyledons of "Cakile americana" (probably *C. edentula*) are "very unequal," but this condition was not observed in cultivated plants nor herbarium specimens. Lubbock's observation that the first leaves of *C. americana* are "very hairy" is also in error.

Flower. The flowers of *Cakile* are typically cruciferous: regular, actinomorphic, tetradynamous, and borne on elongating terminal racemes. The pedicels vary from 1–10 mm long and 0.5–2.5 mm wide, are varyingly divergent, and provide characters, particularly in fruiting material, of taxonomic value. The sepals are borne in two indistinct series with the

outer, lateral pair usually slightly gibbous at the base; they are erect at anthesis and soon deciduous. Sparse, simple trichomes were observed occasionally at the apex of the sepals of all the taxa of *Cakile*. The margins of the sepals are consistently hyaline. In length, they vary from 3–5 mm, and they are commonly dimorphic at the apex, the two laterals being ± straight and acute or obtuse and the two medians tending to being cucullate inward.

The petals, when formed, vary from 5–15 mm long and from distinctly unguiculate in large-flowered taxa to spatulate or obovate in smaller-flowered taxa. Petal size is taxonomically useful although there is considerable overlap and few discontinuities. Table 2 presents the results of measurements of petals from field collections of flowers preserved in FAA or from herbarium specimens (the latter soaked in water or FAA) made under a binocular dissecting microscope with an eyepiece grid. For field collections, measurements were usually made on 10–15 flowers from a population sample of 50 plants. It is my impression that herbarium flowers give consistently smaller values than material preserved in FAA; measurements made on herbarium specimens should, therefore, be scaled slightly upward when compared with FAA-preserved flowers. It is evident that the smallest flowers are found in *Cakile geniculata*, *C. constricta*, and *C. edentula* (and possibly *C. lanceolata* ssp. *alacranensis*) and the largest in *C. maritima* and *C. arctica*, with *C. lanceolata* and *C. arabica* being intermediate. Table 3 presents the results of measurements on petals from growth-chamber cultures; measurements were usually made on 10 plants in each collection. The cultivated plants consistently produced slightly larger flowers than wild plants, as a comparison of Table 2 with Table 3 demonstrates. However, the rankings of the taxa by size remained gen-

TABLE 2. AVERAGE PETAL LENGTH AND WIDTH (MM) IN WILD COLLECTIONS OF CAKILE

Taxon	Collections No.	Plants No.	Length	Range	Width	Range
C. maritima ssp. maritima (Pacific Coast)	10	92	10.9	8.3–13.8	4.6	2.9–6.2
C. arctica*	11	11	8.7	7.5– 9.4	4.2	3.5–5.3
C. lanceolata ssp. fusiformis	9	49	7.5	4.9– 9.4	3.2	2.4–4.2
C. lanceolata ssp. lanceolata	4	22	7.2	5.4– 9.0	3.1	2.1–4.3
C. lanceolata ssp. lanceolata*	25	25	7.1	5.4– 9.0	2.7	1.7–4.2
C. arabica*	5	5	9.1	7.8–11.6	2.6	1.9–3.1
C. lanceolata ssp. pseudoconstricta	1	6	6.5	6.0– 7.0	2.5	2.2–2.8
C. edentula var. edentula (Atlantic Coast)	5	38	6.0	4.6– 7.9	2.2	1.4–3.3
C. edentula var. edentula (Pacific Coast)	5	50	7.2	5.5– 9.7	2.1	1.4–3.2
C. edentula ssp. Harperi	5	39	6.6	5.5– 8.0	2.1	1.5–3.2
C. constricta	6	54	6.5	5.3– 8.0	2.0	1.3–2.6
C. lanceolata ssp. alacranensis*	3	3	6.4	6.2– 7.0	2.0	1.9–2.6
C. edentula var. lacustris	4	30	6.1	5.0– 7.0	2.0	1.5–2.6
C. geniculata	5	44	5.3	4.0– 6.1	1.5	1.2–1.9

*Measurements made on herbarium specimens. All others made on FAA-preserved field collections.

erally the same although *C. constricta* (based on two collections) tended to approach *C. lanceolata* in petal size under the growth-chamber conditions. At anthesis the claws of the petals are erect, enclosed by the erect sepals, and the blades are reflexed about 90°. The blade varies from entire to emarginate within most populations. Elongated, translucent, apparently tubular idioblasts were observed in most petals of many of the collections; these are probably myrosin cells, which Wright (1927) observed in petals of *C. maritima*.

During field work in North America I observed, in populations of *Cakile edentula* ssp. *edentula* on the Atlantic and Pacific coasts and of *C. edentula* ssp. *Harperi*, varying proportions of plants which formed flowers with less than four petals, often none at all. In other respects the flowers appeared normal as did the plants. In five populations of *C. edentula* var. *edentula* on the Pacific Coast the proportion of plants with incomplete flowers varied from 50–100%, in five populations on the Atlantic Coast, 40–90%, in five populations of *C. edentula* ssp. *Harperi*, 10–75%, and in four populations of *C. edentula* var. *lacustris*, 0–15%. Allusions to this phenomenon are rare, both in the literature and in collectors' notes. A collection of *C. edentula* var. *edentula* from Lane County, Oregon (*Cronquist 6104*, GH), bears the comment: "petals none." Meehan (1892) observed that a population of this taxon at Atlantic City, New Jersey, included many plants with incomplete flowers; he also noted that later the same season plants of *C. edentula* in Maine possessed a full complement of petals. In 16 growth-chamber cultures of *C. edentula* I found that flowers were consistently formed with less than four petals, frequently none at all. In four of these cultures, where careful records were kept, I found that flowers borne on axillary racemes late in the season usually had a complete set of petals. Perhaps a temporal shift toward formation of full-petaled flowers occurs in populations of this species. The implications of these observations are discussed in the section on breeding systems.

The flowers of *Cakile* possess four small green nectar glands, two lateral glands subtended by the unpaired stamens and two median glands between and subtending the paired stamens. Hildebrand (1879) and Bayer (1905) provide diagrams of the nectaries in *Cakile*. The lateral nectaries are compressed horizontally and are usually bilobed. The medians are conical or pyramidal and vary from 0.1 to 0.7 mm high. The size of the median nectaries is of some taxonomic value. Small nectaries (0.1–0.3 mm) are characteristic of *C. edentula*, *C. constricta*, and *C. geniculata;* medium nectaries (0.3–0.5 mm) are found in *C. arabica* and three of the four subspecies of *C. lanceolata*; and large nectaries (0.5–0.7 mm) characterize *C. maritima*, *C. arctica*, and *C. lanceolata* ssp. *fusiformis*. Nectary size appears to correlate positively with petal size in general. Measurements of nectar glands can be made easily on fresh or FAA-preserved flowers, but measurements on herbarium flowers, soaked in water or FAA, probably

underestimate the true dimensions since the delicate tissues do not fully expand.

The stamens of *Cakile* are tetradynamous at anthesis but become less so as the flower ages and the unpaired stamens elongate proportionally more than the paired stamens. The filaments are stout, about 0.5 mm wide, and taper abruptly to the point of attachment to the anthers, which are dorsifixed near their base. The bilocular anthers are broadly ovate, slightly cordate basally, and with the connective visible as an apiculate tooth at the apex; they dehisce longitudinally and introrsely in all the taxa though somewhat "latrorsely" in the larger-flowered taxa (e.g., *C. maritima, C. arctica,* and *C. lanceolata* ssp. *fusiformis*). Anther size is of some taxonomic value. Table 4 presents the results of measurements of anthers from field collections of flowers preserved in FAA or from herbarium specimens (soaked in water or FAA) made under a binocular dissecting microscope with an eyepiece grid. For each field collection, measurements were usually made on 10–15 flowers from a population sample of 50 plants. The anthers of the unpaired, lateral stamens consistently tended to be slightly larger than those of the paired, median stamens. The largest anthers occur in *C. maritima, C. lanceolata,* and *C. arabica* and the smallest in *C. edentula* ssp. *edentula* and *C. geniculata,* with *C. edentula* ssp. *Harperi, C. constricta,* and *C. arctica* being intermediate. In general, anther size correlates positively with petal size and nectary size. It was strongly suspected that smaller anthers also produced fewer pollen grains but this was not measured. At anthesis the paired anthers are exserted and overtop the stigma, and the unpaired anthers are lower, within the "cup" of the flower, level with the stigma or below it.

The immature pistil is green, ensiform, and indistinctly articulated transversely. The short-papillose stigma, atop the stylar beak, is hemi-

TABLE 3. AVERAGE PETAL LENGTH AND WIDTH (MM) OF GROWTH-CHAMBER COLLECTIONS OF CAKILE

Taxon	Collections No.	Plants No.	Length	Width
C. lanceolata ssp. fusiformis	4	33	10.9	5.4
C. lanceolata (Bermuda)	1	6	9.7	4.9
C. lanceolata ssp. lanceolata	6	51	9.3	4.9
C. arctica	2	16	9.1	4.7
C. maritima ssp. baltica	1	20	10.4	4.6
C. maritima ssp. maritima (Pacific Coast)	2	20	11.5	4.2
C. constricta	2	11	9.1	3.6
C. edentula ssp. Harperi	2	12	8.6	3.3
C. edentula var. lacustris	3	30	7.8	2.4
C. geniculata	2	26	6.8	2.4
C. edentula var. edentula (Pacific Coast)	1	10	7.8	2.2
C. edentula var. edentula (Atlantic Coast)	4	25	7.6	1.8

TABLE 4. AVERAGE ANTHER LENGTH (MM) IN WILD COLLECTIONS OF CAKILE

Taxon	Collections No.	Plants No.	Lateral Anther	Range	Median Anther	Range
C. maritima ssp. maritima (Pacific Coast)	10	92	1.8	1.5–2.2	1.6	1.4–2.1
C. lanceolata ssp. pseudoconstricta	1	6	1.6	1.6–1.7	1.6	———
C. lanceolata ssp. fusiformis	9	49	1.6	1.3–1.8	1.5	1.3–1.7
C. lanceolata ssp. lanceolata	4	22	1.6	1.4–1.7	1.5	1.4–1.6
C. lanceolata (Bermuda)*	9	9	1.5	1.3–2.2	1.4	1.2–2.0
C. arabica*	5	5	1.5	1.3–1.6	1.5	1.4–1.6
C. lanceolata ssp. lanceolata*	25	25	1.4	1.2–1.7	1.3	1.1–1.7
C. lanceolata ssp. alacranensis*	3	3	1.4	1.3–1.5	1.3	1.2–1.5
C. arctica*	11	11	1.3	1.3–1.4	1.3	1.3–1.4
C. constricta	6	54	1.3	1.1–1.4	1.2	1.0–1.4
C. edentula ssp. Harperi	5	39	1.3	1.0–1.4	1.2	1.0–1.4
C. geniculata	5	44	1.2	0.7–1.3	1.1	0.6–1.3
C. edentula var. edentula (Pacific Coast)	5	50	1.1	0.9–1.4	1.1	0.8–1.3
C. edentula var. edentula (Atlantic Coast)	5	38	1.0	0.4–1.4	0.9	0.4–1.3
C. edentula var. lacustris	4	30	0.9	0.7–1.3	0.9	0.6–1.3

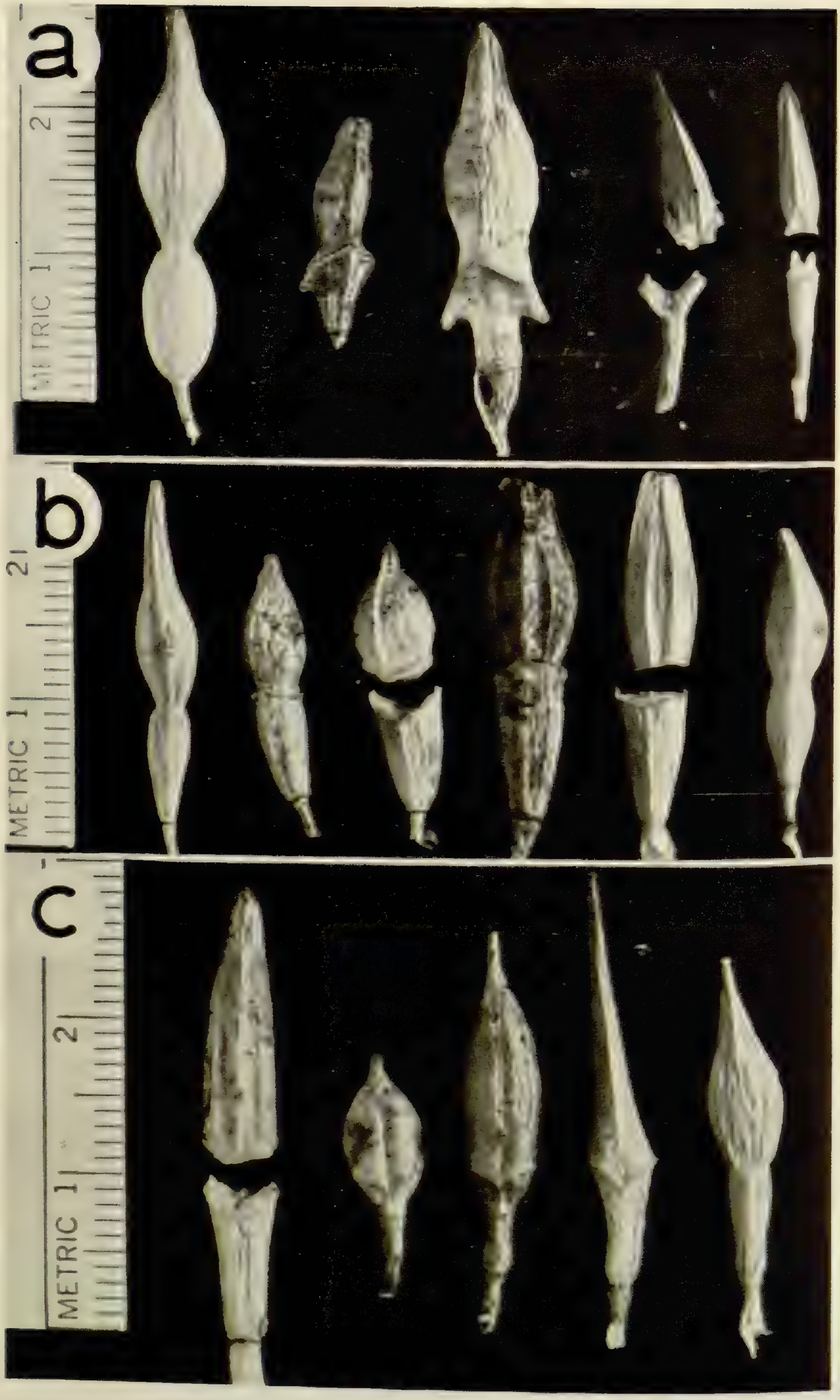
*Measurements made on herbarium specimens. All others made on FAA-preserved field collections.

spherical to slightly bilobed. The articulation of the stigmatic lobes is perpendicular to the plane of the septum. The characteristic lateral horns on the lower segment of the mature fruit of *Cakile maritima* are absent at this early stage. The immature ovary is initially unilocular, with the linear placenta disposed vertically in the elongated chamber and the ovules, usually two, attached in the region of what is to become the articulation between the two fruit segments. A thin elongated septum develops with the ovules on one side of this membrane; a diagrammatic cross section of the young pistil is given by Hannig (1901) and Markgraf (1963). Following fertilization, the ovary wall grows inward between the two ovules, pinching off two segments, the upper one with an erect ovule and the lower with a pendulous one. The small suture which is evident on the articulating surface of the mature fruit segments results from the incomplete fusion of this ingrowth of the ovary wall. The articulating surface is, therefore, not homologous with the septum of other crucifer fruits, nor are the two fruit segments homologous with the two "carpels" of a crucifer fruit. Each mature fruit segment can be split lengthwise into two equal halves, usually revealing a single oblong seed appressed against a thin, papery membrane—that segment's portion of the septum. In *C. maritima,* Wright (1927) observed in immature pistils the regular formation of four ovular primordia, two of which consistently aborted. The chance development and fertilization of one or both of these ovules, in addition to the typically developed two, would explain the infrequent but regular occurrence of two-seeded (and rarely three-seeded) fruit segments in *Cakile*. Wright (1927) interpreted the gynoecium of *Cakile* as tetracarpellary, following Edith Saunder's views on the general

nature of crucifer carpels. More recent opinion inclines toward a bicarpellate interpretation of the cruciferous gynoecium (Carlquist 1969).

Fruit. The distinctive fruit of *Cakile* is an indehiscent, hard-corky ("nucamentaceous"), two-segmented silique. Zohary (1948) described the fruit as a special case of his "valvo-nucamentoid" type and considered the upper and lower segments to be homologous to, respectively, the "stylar" and "valvar" portions of fruits typical of the tribe Brassiceae. The upper segment is deciduous; the lower remains attached to the raceme. The fruit is thus an example of what Zohary has termed "heteromericarpy" (van der Pijl 1969). Both segments are (falsely) one-loculed and usually one-seeded (although a septum develops, seeds are formed on only one side of it). Size and shape of the fruit provide important characters for distinguishing infrageneric taxa (Plate 1). Features pertaining to the articulating surface between the two fruit segments have some taxonomic significance although certain characters, such as number of small teeth on the surface of the lower segment, have been emphasized without regard to their variation within populations. The number of seeds per segment has, unfortunately, also been used as a taxonomic character, particularly by Small (1903, 1913, 1933), again without regard to the variation within populations. Characteristics which have been found to be taxonomically valuable include the shape of the beak, whether retuse, obtuse, or sharply acute at the apex; the length of the segments; the outline of the upper segment in cross-section, whether distinctly four-angled, eight-ribbed, or ± sulcate; the development of a membranous margin at the base of the upper segment; the presence of lateral horns on the lower segment; the shape of this segment, whether cylindric or distinctly broadened at the top; the consequent width of the articulating surface; and the development of various projections on this surface. While fruit characters are among the most reliable in the genus, nearly all of them intergrade to some degree; and there are few sharp discontinuities between the taxa. This is the case with nearly all the characters in *Cakile* and it is perhaps to be expected in an assemblage of (primarily) strand plants with contiguous geographic ranges and great dispersibility. One species which can be readily identified from its fruits alone is *C. arabica,* which is the only geographically isolated species in the genus.

The averages resulting from measurements of pedicel length (of fruits) and fruit length (and length of the constituent lower and upper segments, usually), made on herbarium specimens, are presented in Table 5, with the taxa ranked by decreasing fruit length. For comparison, measurements to the nearest half-millimeter were made only on one of the four lowermost mature fruits of a raceme (usually the main raceme) for which the segments of the fruit were judged to be fertile. In this way, confounding errors resulting from variation along a raceme or from variation between fertile and sterile segments were avoided. In a few cases, when none of


a
b
c
METRIC 1
2
21

the four lowermost fruits was fully fertile, measurements were made on one fertile segment (the other being recognizably sterile from its smaller size). Consequently, the combined values for the lower and upper segments may not always equal the value for fruit length for a particular taxon in Table 5. For each value for fruit length, the coefficient of variability, V (Simpson, Roe & Lewontin 1960), was calculated from the mean and standard deviation to provide an estimate of the amount of variation in the samples of collections measured. In addition, for many pairs of values for fruit length, Student's t-test was calculated to assess the statistical significance of the differences between taxa.

For the most part, the longest fruits and the longest pedicels are found in *Cakile arctica* of Iceland, the Faeroes, and northern Scandinavia. These sea rockets have often been treated as conspecific with *C. edentula* var. *edentula* of the Atlantic Coast of North America, but the latter is clearly distinct and possesses shorter fruits, the differences between the two being highly significant statistically ($P < 0.001$). The fruits of *C. edentula* ssp. *Harperi* are nearly as long as those of *C. arctica* but are clearly distinguishable morphologically.

Cakile edentula var. *lacustris* of the Great Lakes bears longer fruits than does *C. edentula* var. *edentula* of the Atlantic Coast, and the difference is statistically very significant ($P < 0.001$), as is the difference in fruit length between *C. edentula* var. *lacustris* and the Great Lakes collections of *C. edentula* var. *edentula*. Patman and Iltis (1961) also demonstrated a rather clear separation of the two varieties by fruit size in Wisconsin collections. Surprisingly, the difference in fruit length between Atlantic Coast *C. edentula* var. *edentula* and the Great Lakes collections of this variety is also very significant ($P < 0.001$). The difference could have resulted from a bias in measuring, longer fruits being considered automatically as *C. edentula* var. *lacustris*, thus leaving a residue of small-fruited typical *C. edentula*. Such a bias, however, would most likely have resulted in a much higher value of V for *C. edentula* var. *lacustris* than was found. The Great Lakes material of *C. edentula* var. *edentula* does not appear to differ in any other respect from typical Atlantic Coast material, and I would attribute the difference in fruit length to a founders' effect.

The difference in fruit length between *Cakile edentula* ssp. *edentula* var. *edentula* and *C. edentula* ssp. *Harperi* of the Atlantic Coast is also highly significant statistically ($P < 0.001$). Intermediates do occur, however, in the transition zone between the two along the Outer Banks of North

PLATE 1. Fruits of *Cakile* A. Left to right: *C. arctica* (Rodman 107); *C. maritima* ssp. *baltica* (Rodman 182); *C. maritima* ssp. *maritima* (Rodman 78); *C. maritima* ssp. *euxina* (Stojanoff s.n.); *C. arabica* (Dickson 573). B. Left to right: *C. edentula* var. *lacustris* (Rodman 132); *C. edentula* var. *edentula* (Rodman 96—segments united and separated); *C. edentula* ssp. *Harperi* (Rodman 45—segments united and separated); *C. constricta* (Rodman 60). C. Left to right: *C. geniculata* (Rodman 64); *C. lanceolata* ssp. *alacranensis* (Fosberg 41910); *C. lanceolata* ssp. *fusiformis* (Rodman 53); *C. lanceolata* ssp. *lanceolata* (Rodman 114); *C. lanceolata* ssp. *pseudoconstricta* (Rodman 57).

TABLE 5. AVERAGE PEDICEL AND FRUIT LENGTH (MM) IN CAKILE

Taxon or Area	Collections No.	Pedicel	Range	Lower Segment	Range	Upper Segment	Range	Fruit	Range	V*
C. arctica	10	6.5	5 –10	8.5	6 –11	16.3	14 –20	24.8	21 –31	12.4
C. lanceolata ssp. lanceolata	134	2.7	1.5– 4	7.2	5 –10	17.6	13 –24	23.8	19 –31	9.6
C. edentula ssp. Harperi	49	3.6	2 – 5	8.7	7.5–10	15.1	12 –19.5	23.8	20 –29	9.3
C. geniculata	32	3.8	2 – 5	8.2	6 –11	15.7	13 –18	23.6	20 –27	7.6
Mexico: Gulf collections, all taxa	15	3.0	1.5– 4.5	7.5	5 –10	15.3	12 –18	21.8	15 –27	17.9
C. lanceolata (Bermuda only)	19	3.2	2 – 4	7.3	5 – 9	14.7	10 –20	21.2	14 –29	18.7
Louisiana collections, all taxa	14	3.5	2 – 4.5	7.2	6 –10	13.9	10.5–18	21.0	17 –25	14.8
C. edentula var. lacustris (Great Lakes)	147	4.4	2 – 8	7.7	5 –12	13.6	11 –18	21.0	16 –26	9.8
C. lanceolata ssp. fusiformis (so. Fla. only)	56	2.8	2 – 4	7.1	5 –10	13.9	10.5–18	20.8	16 –25.5	10.8
Central American collections, all taxa	21	2.5	1.5– 3	7.1	4 –10	14.6	12 –18	19.8	13 –26	18.7
C. maritima ssp. euxina (Black Sea only)	7	3.1	2 – 4.5	—	—	—	—	19.3	17 –21	7.8
C. maritima ssp. maritima (Pacific Coast only)	91	3.1	1.5– 7	—	—	—	—	19.2	14 –27	11.6
C. maritima ssp. maritima (Mediterranean only)	53	2.9	1.5– 6	—	—	—	—	18.9	14 –27	13.7
C. lanceolata ssp. pseudoconstricta (SW Fla. only)	32	3.1	1.5– 5	6.5	5.5– 8	12.0	9 –17	18.5	15 –24	11.0
C. constricta (Gulf of Mexico only)	65	3.9	2.5– 7	6.4	5 – 8.5	12.2	9 –15	18.2	14 –22	9.4
C. edentula var. edentula (Australia only)	41	3.3	2 – 6	6.8	5 –11	11.0	8 –13	17.9	14 –21.5	10.5
C. edentula var. edentula (Pacific Coast only)	127	3.2	1.5– 5.5	7.1	5 –11.5	10.8	8 –16	17.9	13.5–27.5	11.2
C. edentula var. edentula (Atlantic Coast only)	218	2.8	1.5– 8	7.7	5 –10	10.3	7 –15	17.9	12 –24	10.9
C. lanceolata ssp. pseudoconstricta (Texas only)	25	3.8	3 – 5	6.3	5 – 8	11.2	9 –14	17.4	15 –21	9.4
C. maritima ssp. baltica	36	4.2	3 – 5	—	—	—	—	17.3	12 –27	15.4
C. arabica	12	2.0	1.5– 3	4.8	3 – 5	12.0	10 –16	16.8	14 –21	12.6
C. lanceolata ssp. alacranensis	8	2.3	2 – 3.5	5.1	5 – 6	10.3	9 –13	15.4	14 –19	12.7
C. edentula var. edentula (Great Lakes)	22	2.3	1.5– 3	6.8	6 – 9	8.6	6.5–11	15.1	12.5–18	9.7

*Coefficient of variability of the value for fruit length.

TABLE 6. AVERAGE PEDICEL AND FRUIT LENGTH (MM) IN CAKILE EDENTULA VAR. EDENTULA BY REGION

Region	Collections No.	Pedicel	Range	Lower Segment	Range	Upper Segment	Range	Fruit	Range	V*
Quebec	26	3.0	2 –5	6.8	5.5– 9	10.9	8.5–15	17.4	14 –23	12.5
Nova Scotia, Newfoundland, New Brunswick, Prince Edward Island	34	2.9	1.5–4	7.6	5 –10	10.2	7 –13.5	17.5	13 –21.5	11.0
Maine, New Hampshire, Massachusetts	43	3.1	2 –5	7.5	5 –10	9.9	7 –13	17.1	12 –22	12.9
New York, Connecticut, Rhode Island	34	2.5	1.5–4	8.0	5.5–10	9.9	8 –12.5	17.9	14 –22	10.7
New Jersey	44	2.9	1.5–8	8.2	6 –10	10.6	7.5–14	18.7	14 –24	10.5
Delaware, Maryland, Virginia, North Carolina	37	2.6	2 –4	8.0	6 –10	10.6	8.5–14	18.6	15.5–22	8.3

*Coefficient of variability of the value for fruit length.

TABLE 7. AVERAGE PEDICEL AND FRUIT LENGTH (MM) IN CAKILE LANCEOLATA SSP. LANCEOLATA BY REGION

Region	Collections No.	Pedicel	Range	Lower Segment	Range	Upper Segment	Range	Fruit	Range	V*
Cayman Island	9	3.1	2 –4	6.6	5– 8	13.1	11–15	20.1	17–22	–
Cuba	11	2.6	2 –3	7.0	6– 9	15.9	14–18	22.7	19–26	10.4
Jamaica	33	2.7	2 –4	6.8	5– 9.5	16.3	13–18.5	22.3	19–26	9.1
Hispaniola	8	2.4	2 –3.5	7.3	6–19	17.4	15–20	24.6	22–27	6.1
Bahamas	34	2.8	1.5–4	7.3	5–10	17.6	14–22	24.2	19–29	12.0
Puerto Rico	16	3.0	2 –4	7.1	6– 8	18.3	15–23	24.4	20–31	10.6
Lesser Antilles	32	2.5	2 –3.5	7.6	6–10	18.4	15–24	24.9	22–29	7.7
Bermuda	19	3.2	2 –4	7.3	5– 9	14.7	10–20	21.2	14–29	18.7

Carolina. Within *C. edentula* var. *edentula* on the Atlantic Coast, there appears to be no trend toward longer fruits (approaching *C. edentula* var. *lacustris*) in collections from North Carolina northward to the Gulf of the St. Lawrence River, as is evident from Table 6. In fact, the average fruit length for the 26 collections measured from Quebec was the smallest encountered. Sporadic collections in the Gulf of the St. Lawrence appear to be of *C. edentula* var. *lacustris*, but no evidence for a cline in fruit length has been detected.

The difference in fruit length between *Cakile lanceolata* ssp. *fusiformis*, measured from collections from Dade, Monroe, and Collier Counties in southern Florida, and *C. constricta*, measured from collections from the Florida panhandle, Alabama, and Mississippi, is also highly significant ($P < 0.001$). Collections from the intermediate region in Florida (Lee to Pinellas Counties) are relatively homogeneous (V=11.0) and not significantly different from *C. constricta*, but they do differ significantly ($P < 0.001$) from *C. lanceolata* ssp. *fusiformis*. Furthermore, several Texas collections which are clearly not *C. geniculata* appear to be homogeneous in fruit length (V=9.4), similar to *C. constricta* in fruit morphology, and significantly different ($P < 0.001$) from *C. lanceolata* ssp. *fusiformis*. These collections from southwestern Florida and Texas are treated as ***C. lanceolata*** **ssp. *pseudoconstricta*.**

The difference in fruit length between *Cakile constricta* (measured from Gulf Coast collections) and *C. geniculata* is statistically significant ($P < 0.001$). Measurements on collections from Louisiana, where the two species are sympatric, give a correspondingly high value for V (14.8), indicating considerable variability, and an intermediate value for fruit length. Hybridization is, I suspect, occurring here and in adjacent eastern Texas; evidence for this is presented in the section on hybridization.

Heterogeneity is also indicated by high values for V in collections from Mexico (the Gulf Coast from Tamaulipas to Yucatan) and from Central America (Quintana Roo to Honduras). In Mexico, the transition from long-fruited *Cakile geniculata* in Tamaulipas to the very short-fruited *C. lanceolata* ssp. *alacranensis* of northern Yucatan explains in part the intermediate value for fruit length and the high V (17.9). The situation is further confounded by the presence of a few collections each of *C. lanceolata* ssp. *lanceolata*, ssp. *fusiformis*, and ssp. *pseudoconstricta*. Unfortunately, the paucity of collections from this region precludes any clear formulation of the geographic distributions of these taxa along the Gulf Coast. In Central America, the heterogeneity in fruit length (V=18.7) arises from the transition from *C. lanceolata* ssp. *alacranensis*, through *C. lanceolata* ssp. *fusiformis* along the eastern coast of the Yucatan peninsula, to typical *C. lanceolata* in Honduras and Panama.

The fruit length of typical *Cakile lanceolata*, measured from collections from Cuba, Jamaica, the Bahamas, Hispaniola, Puerto Rico, and the Lesser

Antilles, is significantly different from that of southern Florida *C. lanceolata* ssp. *fusiformis* ($P < 0.001$) and from the average for the Bermuda collections. The heterogeneity in the latter (V=18.7) arises from a mixture of typical *C. lanceolata* with *C. lanceolata* ssp. *fusiformis* and with slightly distinctive local forms. Pobedimova (1964) remarked upon the heterogeneity of Bermudan collections, and I found a distinctive seed composition in the two collections analyzed for glucosinolates. Within the Antillean and Bahamian collections of *C. lanceolata* ssp. *lanceolata*, which are relatively homogeneous for fruit length (V=9.6), there appears a slight trend from shorter-fruited forms in Jamaica and Cuba in the west to longer-fruited ones in the Lesser Antilles in the southeast, as is evident from Table 7. The trend is even clearer for the length of the upper, deciduous fruit segment. Possibly selection for longer fruits, which may be more buoyant, has occurred in populations in the Lesser Antilles, the southeastern extremity of the range of the species and of the native range of the genus in the New World. This selection may have occurred in response to migration into this area by sea or in response to pressures for maintaining gene flow between small island populations. Regardless of such speculations, the observed differences in fruit length are gradual and continuous and do not warrant nomenclatural distinction.

The average fruit length of Mediterranean collections of *Cakile maritima* ssp. *maritima* is not statistically different from that of the naturalized members of this subspecies from the Pacific Coast of North America. The difference in fruit length between Mediterranean *C. maritima* ssp. *maritima* and Baltic Sea *C. maritima* ssp. *baltica*, however, is statistically significant ($P < 0.01$). The latter subspecies also possesses longer pedicels. Measurements of fruit length were not made on Western European collections because the majority of those available for study bore fruits with reduced, sterile lower segments (the upper segments then usually remaining attached to the raceme, apparently not readily deciduous). Of 44 Western European collections of *C. maritima*, 41 (93%) bore fruits with aborted lower segments whereas 58 (95%) of the 61 Mediterranean collections bore normally fertile fruits. Pobedimova (1963, 1964) treated the sea rockets of Western Europe as the species *C. monosperma*, with characteristically aborted lower fruit segments, and restricted the application of the name *C. maritima* to Mediterranean plants. Ball (1964a, b), on the other hand, considered the Western and Southern European sea rockets as subspecies of *C. maritima*, ssp. *maritima* on the Atlantic Coast and ssp. *aegyptiaca* in the Mediterranean. He (1964a) remarked that "[p]lants with some or all of the fruits with the lower segment undeveloped certainly occur throughout Western and Southern Europe, and are indistiguishable from *C. maritima*." Nonetheless, a clear geographic separation was evident to me, and Pobedimova's parallel judgment was surely inspired by a study of many more herbarium collections. It appears

highly probable that the "monosperma" condition is a characteristic of many populations of Western European *C. maritima*. Field studies of natural populations are needed to determine the extent of this condition. In other respects, the Western European sea rockets do not differ obviously from Mediterranean *C. maritima* and, when doubly fertile fruits are formed, the plants are morphologically indistinguishable from much Mediterranean material. Hence, I have chosen to treat the Western European and Mediterranean sea rockets as the one variable taxon, *C. maritima* ssp. *maritima*.

Seeds. The seeds of *Cakile* are dimorphic, the upper, deciduous fruit segments bearing seeds slightly larger and heavier on the average than the lower segments. The dimorphism is an example of what Harper, Lovell, and Moore (1970) have termed "somatic dimorphism," in contradistinction to genetic polymorphism. The seeds are usually oval or ellipsoid to slenderly oblong, compressed longitudinally, variously brown or bronze, and ± smooth or punctilate (Murley 1951). The cotyledons are usually accumbent, but seeds with oblique to incumbent cotyledons were regularly, albeit rarely, observed in population samples of all the taxa investigated. They appeared to be rather more common in *C. geniculata* and *C. lanceolata* than in the other species. While each fruit segment is typically one-seeded, I regularly observed in population samples that both segments might be multispermous (usually two-seeded) or abortive in a small proportion of cases (up to 10%). Lower fruit segments tended to be multispermous or abortive more often than upper segments, an observation also made by Barbour (1970a) for *C. maritima* ssp. *maritima* in California. Three-seeded fruit segments were quite rare, and only one four-seeded (lower) segment was seen (in *C. edentula* var. *edentula*) from the several hundreds that were shelled.

Average seed weight for all the taxa of *Cakile* investigated is presented in Table 8, with the taxa ranked in decreasing order by weight. For each collection (usually a population sample of fruits from 50 plants but occasionally a single plant or a sample with a few plants) 12–50 seeds were weighed on a Mettler P120 Electronic Balance and a value for individual seed weight was extrapolated; the results from several collections were then averaged for each taxon. The heaviest seeds are found in *C. arctica* and *C. edentula*, the lightest in *C. lanceolata* and *C. constricta; C. maritima* and *C. geniculata* are intermediate. Not enough seeds of *C. arabica* were available, but these are typically quite small and presumably would be among the lightest in the genus. Seeds from upper fruit segments are, on the average, consistently heavier than those from lower fruit segments. The Old and New Worlds' northernmost taxa—*C. arctica* and *C. edentula*—averaged heavier seeds than more southern taxa. Larger, heavier seeds in northern taxa may represent an adaptation to harsher environments.

TABLE 8. AVERAGE SEED WEIGHT (MG) OF CAKILE

Taxon	Collections No.	Lower Seeds	Range	Upper Seeds	Range
C. arctica	1	13.2	——	14.8	——
C. edentula ssp. Harperi	9	10.7	8.4–12.6	12.3	9.6–14.0
C. edentula var. edentula (Pacific Coast)	4	9.2	7.8–11.2	12.2	9.6–15.8
C. edentula var. edentula (Atlantic Coast)	19	9.2	7.2–11.4	9.5	7.2–12.6
C. maritima ssp. maritima (Pacific Coast)	8	6.5	5.2– 7.4	8.4	6.8–10.6
C. maritima ssp. baltica	4	6.3	5.6– 6.7	8.2	7.6– 8.9
C. edentula var. lacustris	3	5.9	5.6– 6.2	7.7	5.4–10.4
C. geniculata	6	6.4	5.2– 8.8	7.0	5.2–10.6
C. lanceolata ssp. lanceolata	12	4.5	3.6– 5.6	5.4	4.2– 6.8
C. lanceolata (Bermuda)	2	4.0	3.8– 4.2	4.9	4.6– 5.2
C. constricta	5	3.9	2.8– 4.6	4.8	3.6– 5.8
C. lanceolata ssp. pseudoconstricta	3	4.0	3.8– 4.2	4.6	——
C. lanceolata ssp. fusiformis	9	3.6	2.4– 4.4	4.4	3.2– 5.8
C. lanceolata ssp. alacranensis	1	——	——	4.0	——

Published reports of seed weights in *Cakile* generally agree with those presented here although most researchers do not distinguish upper and lower seeds (Löve 1963; Mikolajczak *et al.* 1961). The values for *C. maritima* in the literature show considerable variation. Miller *et al.* (1965) reported 4.2 mg/seed for *C. maritima* (ssp. *maritima*, most certainly) from Israel, without distinguishing upper and lower seeds. Binet (1961) reported 4.25 mg/upper seed for *C. maritima* (ssp. *maritima*, most certainly) from western France [the value of 2.4 mg/seed attributed to Binet by Barbour (1970a) results from a misinterpretation of Binet's histogram for upper fruit weight]. For *C. maritima* (ssp. *maritima*, most likely) from England, Guppy (1912) reported 12.96 mg/upper seed and 4.5 mg/lower seed, which is an anomalously great difference. Becker (1912) reported 9.32 mg/upper seed and 8.54 mg/lower seed for *C. maritima* (ssp. *baltica*, most likely) from the Baltic Sea coast, values only slightly greater than those I obtained for this taxon. Becker's results were repeated by Salisbury (1942) and also by Barbour (1970a) who attributed them to Salisbury. For *C. maritima* ssp. *maritima* in California, Barbour (1970a) reported 8.1 mg/upper seed and 6.0 mg/lower seed, in close agreement with the results in Table 8. Seed weight in naturalized *C. maritima* ssp. *maritima* appears to be greater than in native *C. maritima* ssp. *maritima*, therefore. The possibility of geographic or clinal variation in seed weight in Old World *C. maritima* ssp. *maritima* has not been investigated.

The results of measurements of seed size for taxa of *Cakile* are presented in Table 9. For each collection (usually a population sample of fruits from 50 plants) 25–45 seeds were measured under a binocular dissecting microscope with an eyepiece grid, and the averages were calculated; an average value for several collections was then computed. The values for

seed dimensions correlated positively with those for seed weight. The largest seeds are found in *C. arctica* and *C. edentula,* the smallest in *C. lanceolata* and *C. constricta; C. maritima* and *C. geniculata* are more or less intermediate.

Published accounts of seed size in *Cakile* (Murley 1951; Vaughan & Whitehouse 1971) are in general agreement with those I obtained.

Raceme. The raceme in *Cakile* is terminal and ebracteate; occasionally the first flower will be subtended by a small, linear leaf. In *C. geniculata* the fruiting racemes vary from one to two dm in length, rarely longer, and are distinctly geniculate. The diameter of the rachis and of the fruiting pedicel at a bend are usually ± equal. A tendency toward a geniculate infructescence is found in *C. edentula* ssp. *Harperi* and, to a slighter extent, in *C. edentula* ssp. *edentula.* Both of these taxa also produce racemes varying from one to two dm in length, occasionally longer. The length of the raceme in *C. constricta* and *C. arctica* varies over a wider range (one to four dm) but is typically two to three dm long. In *C. maritima* and *C. lanceolata* fruiting racemes typically exceed two dm and

TABLE 9. AVERAGE SEED LENGTH AND WIDTH (MM) IN CAKILE

Taxon	Collections No.	Lower Seeds Length	Lower Seeds Width	Upper Seeds Length	Upper Seeds Width
C. arctica	2	(4.5)5.3(6.2)	(2.4)2.8(3.6)	(4.4)5.5(6.8)	(2.1)2.8(3.2)
C. edentula ssp. Harperi	7	(3.5)5.1(6.1)	(1.6)2.3(2.9)	(4.5)5.4(6.5)	(1.6)2.5(3.2)
C. maritima ssp. baltica	1	(3.5)4.6(6.0)	(1.6)2.1(2.5)	(5.0)5.3(5.5)	(2.0)2.1(2.5)
C. edentula var. edentula (Atlantic Coast)	9	(3.9)4.9(6.4)	(1.6)2.3(3.1)	(4.2)5.2(6.1)	(2.1)2.7(3.3)
C. edentula var. edentula (Pacific Coast)	2	(4.4)4.9(6.3)	(1.6)2.3(3.1)	(4.4)5.2(6.2)	(1.9)2.7(3.4)
C. edentula var. lacustris	3	(3.6)4.5(5.2)	(1.4)1.8(2.4)	(3.8)4.7(5.5)	(1.8)2.3(2.7)
C. maritima ssp. maritima (Australia)	1	(3.6)3.9(4.6)	(1.6)2.1(2.5)	(4.1)4.7(5.5)	(2.0)2.3(2.6)
C. maritima ssp. maritima (Pacific Coast)	3	(3.4)4.1(5.3)	(1.2)2.0(2.5)	(3.4)4.7(5.5)	(1.6)2.2(3.0)
C. geniculata	3	(4.1)4.7(5.3)	(1.4)1.7(2.2)	(3.9)4.7(5.4)	(1.4)1.7(2.3)
C. lanceolata ssp. lanceolata	6	(3.4)4.3(5.3)	(1.3)1.5(2.1)	(3.9)4.6(5.3)	(1.5)1.8(2.4)
C. constricta	5	(3.3)4.1(4.9)	(1.3)1.6(1.9)	(3.4)4.2(5.1)	(1.3)1.6(2.0)
C. lanceolata ssp. pseudoconstricta	2	(3.4)4.1(4.7)	(1.3)1.5(1.7)	——	——
C. lanceolata ssp. fusiformis	8	(3.2)3.9(5.1)	(1.1)1.5(2.2)	(3.2)4.0(5.1)	(1.5)1.8(2.4)
C. lanceolata (Bermuda)	2	(2.7)3.7(4.6)	(1.4)1.6(2.1)	(3.2)3.8(4.6)	(1.6)1.9(2.2)
C. lanceolata ssp. alacranensis	1	——	——	(3.4)3.7(4.0)	(1.5)1.6(1.6)

frequently exceed three dm in length. The length of infructescences in *C. arabica* varies between one and three dm.

Under uniform environmental conditions (growth chamber with 16 hrs of light daily) the taxa produce varying numbers of flowers on an individual raceme with averages generally correlated positively with infructescence length, as demonstrated in Table 10, where the taxa are ranked in increasing order by number of flowers/raceme. *Cakile edentula* and *C. geniculata*, under these conditions, typically produced fewer than 30 flowers on a raceme. *Cakile constricta* usually produced 10–20 more flowers on somewhat longer racemes. In the remaining taxa investigated, *C. maritima*, *C. lanceolata*, and *C. arctica*, the racemes often bore more than 40 flowers; indeed, the values given in Table 10 underestimate the potential in these taxa since counts were often made when the plants were still flowering. In some instances more than 100 flowers were produced on single racemes. Barbour (1970d) reported longer racemes and more flowers/raceme on plants of *C. maritima* grown in growth chambers and compared with Oregon-derived *C. edentula*. Salisbury (1942) reported finding a plant of *C. maritima* ("above the average in size") which had produced (on several racemes, of course) 5628 fruits! The implications of these data for the reproductive biology of the taxa are discussed in the section on breeding systems.

Pollen

The pollen grains of *Cakile* are tricolpate as are most in the Cruciferae (Erdtman 1952). Mounted in methylene blue or acetocarmine, they appear spherical or oblate-spheroidal and exhibit a coarse reticulum when viewed through a light microscope. A photomicrograph of a pollen grain

TABLE 10. NUMBER OF FLOWERS/MAIN RACEME AT OR NEAR END OF GROWTH CYCLE UNDER UNIFORM GROWTH-CHAMBER CONDITIONS IN TAXA OF CAKILE

Taxon	Cultures No.	Plants No.	Average	Range
C. geniculata	2	8	16.4	11– 22
C. edentula ssp. Harperi	1	3	21.3	18– 25
C. edentula var. edentula	3	21	24.7	13– 34
C. edentula var. lacustris	2	15	25.0	19– 37
C. constricta	2	9	39.6	31– 49
C. maritima ssp. baltica	1	6	41.6	28– 56
C. lanceolata ssp. lanceolata	5	25	42.3	25– 73
C. arctica	2	11	43.0	23– 59
C. lanceolata ssp. fusiformis	2	7	46.6	19–108
C. lanceolata (Bermuda)	1	3	69.7	56– 78
C. maritima ssp. maritima	1	6	103.0	62–150

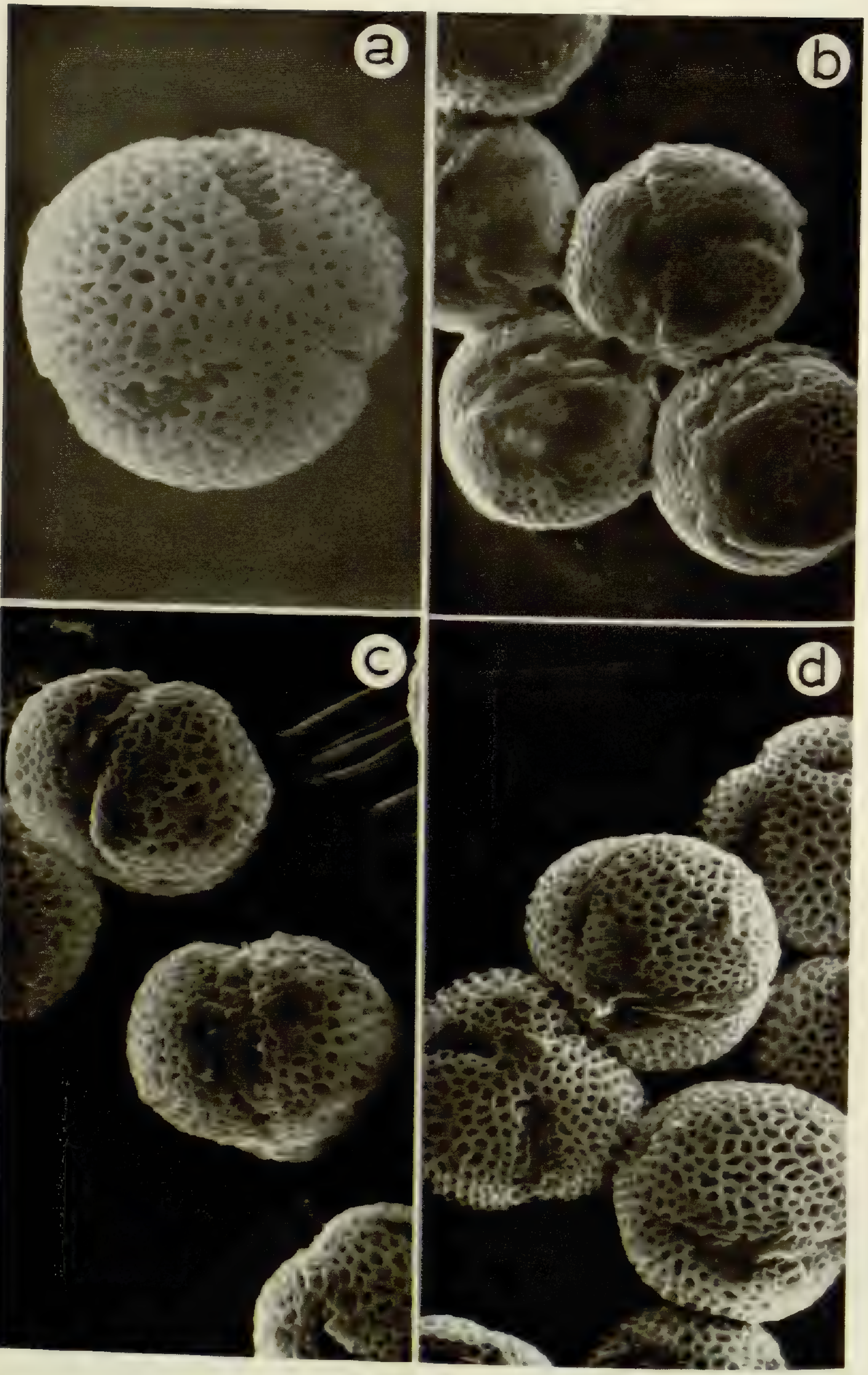


PLATE 2. Scanning electron photomicrographs of pollen of *Cakile*. Fig. A. *C. maritima* ssp. *maritima* (Rodman 82), 2620×, from FAA-preserved flowers; Fig. B. *C. maritima* ssp. *maritima* (Rodman 82), 1200×, water mounted; Fig. C. *C. edentula* var. *edentula* (Rüdenberg s.n.), 1360×, water mounted; Fig. D. *C. lanceolata* ssp. *lanceolata* (Hodgdon & Pike 15583), 1300×, water mounted.

of *C. maritima* can be found in Markgraf's work (1963, fig. 282). Greater detail is observable with the scanning electron microscope (Plate 2). For this study, non-acetolyzed pollen from herbarium specimens or from flowers preserved in FAA was mounted on small aluminum studs with double-stick tape, undercoated with carbon, and plated with a palladium-gold alloy and then observed with an AMR Model 900 instrument. Grains which had been mounted in a drop of distilled water, particularly those of *C. maritima* (collection 82 from California), showed a coating of presumably oily material over most of their surface; such oily deposits are typical of entomophilous species (Faegri & Iversen 1964). Grains of this same collection from flowers preserved in FAA showed much less of this oily substance over their exine; the preservative had apparently dissolved most of it. Collections of *C. maritima* ssp. *maritima*, of *C. edentula* var. *edentula* (*Rüdenberg s.n.*, GH), and of *C. lanceolata* ssp. *lanceolata* (*Hodgdon & Pike 15583*, GH) were examined with the SEM and the pollen of all was found to be similar. The grains appeared spherical to slightly oblate when initially mounted in a drop of water. Experience with other taxa (e.g., *Brassica* spp.) suggests that grains mounted dry would appear prolate, the longer axis then being polar and not equatorial. At magnifications of ca. 7000×, the columellae are often clearly visible, and the surface of the furrows appears distinctly granular. The lumina of the brochi are unequal in size, often large, and irregular in outline. The pollen of *Cakile* is very similar to that of *Brassica*, *Raphanus*, *Rapistrum*, *Crambe*, and *Erucaria* (unpublished results) with which it is associated tribally or subtribally.

After a study of the pollen from 91 herbarium specimens of *Cakile edentula* and *C. maritima*, Green (1955) concluded that it was "impossible to differentiate between the species of *Cakile* by using pollen grain size; this is an apparent exception to the general rule that increase in ploidy is reflected by an increase in pollen grain size." Green's investigation had been prompted by the publication of Löve and Löve (1947) in which they announced that the Icelandic sea rockets, considered by them at that time as typical *C. edentula*, were tetraploids. This count, appearing in the standard chromosome atlases (Darlington & Wylie 1955; Delay 1951), undoubtedly created the impression that *C. edentula* of the Atlantic Coast of North America was a tetraploid. As shown in the section on chromosome counts, however, all the sea rockets, including the Icelandic plants, share the same diploid chromosome number. Green's study, therefore, did not constitute a true test of the generalization that polyploids exhibit a larger cell size than their diploid relatives (Stebbins 1950).

Green (1955) provided valuable data on pollen grain size in *Cakile edentula*, *C. maritima*, and *C. lanceolata*. For the former two he reported an average size of $35.1\mu \times 32.1\mu$ and for the latter, based on four specimens, $34.0\mu \times 31.6\mu$. These results are consonant with those presented in

Table 11. The measurements were made on only a few grains each from growth chamber plants of the six taxa. The grains were mounted in methylene blue or acetocarmine and measured at 430 × with an eyepiece micrometer; small, aborted grains, encountered in varying numbers in the samples, were not included. The slightly higher values in Table 11, compared with those of Green, are probably due to the different mounting

TABLE 11. POLLEN GRAIN SIZE IN CAKILE (μ)

Taxon	Collection	Axes	
		Equatorial	Polar
C. arctica	105	38.4	33.8
	107	36.0	31.2
C. edentula ssp. edentula var. edentula	26	40.8	33.6
C. edentula ssp. Harperi	24–2	38.4	31.2
C. geniculata	25–2	43.2	31.2
C. lanceolata ssp. fusiformis	W–9138	36.0	32.4
	W–9138–2	40.8	33.6
C. lanceolata ssp. lanceolata	R–s.n.–2	38.4	32.4

media used. Compared to the values for pollen grain size in the Cruciferae of 20–30μ given by Erdtman (1952), those of *Cakile* appear to be among the larger grains of the family.

CHROMOSOME NUMBERS

The Cruciferae, for which chromosome studies have contributed notably to an understanding of relationships, continue to elicit broad cytological investigations (Rollins & Rüdenberg 1971; Harberd 1972) following the distinguished precedent established by Manton (1932). Within the genus *Cakile*, however, chromosome data are of little taxonomic or phylogenetic value. As Table 12 amply testifies, reports of counts in this genus are consistently the same (n=9, $2n$=18) with a single, perplexing exception.

The exceptional count, of n=18, $2n$=36, was published by Löve and Löve (1947) for plants from Iceland which they treated as *Cakile edentula* ssp. *typica* (Fern.) Hultén. Judging from a high frequency of quadrivalents, these researchers concluded that *C. edentula* in Iceland was an autotetraploid. Unfortunately, other authors, extrapolating from the single report by Löve and Löve (1947), have stated that the North American *C. edentula* is a tetraploid (Allen 1952; Lousley 1953; Green 1955). This count was repeated in later publications (Löve & Löve 1948, 1956); however, in 1954 Löve listed $2n$=18 for *C. edentula*, perhaps reflecting the report by Kruckeberg (1948) for *C. edentula* in California.

In their 1956 publication, Löve and Löve reported that they had found diploid, tetraploid, and octoploid numbers in root tip preparations of the Icelandic plants on which they had published earlier but had observed only the tetraploid condition in pollen mother cells. The diploid state was most frequent in some of the root tips studied, which they interpreted as somatic haploidy. They also remarked that the Icelandic plants differed slightly, morphologically, from the American *C. edentula*. Later, Löve and Löve (1961a) recognized the Icelandic sea rockets as a distinct subspecies, *C. edentula* ssp. *islandica* (Gandoger) Löve & Löve, and under this new combination they repeated their tetraploid count of $2n$=36 (Löve & Löve 1961b). Subsequent investigations of this taxon (treated here as *C. arctica*) both in Iceland and in other parts of its range have demonstrated that the plants are diploid, with $2n$=18, as in all other sea rockets studied. This diploid count was used by Löve (1970) in his recent Icelandic flora where the plants are treated as *C. edentula* var. *islandica* (Gandoger) Löve.

For sea rockets identified as *Cakile edentula* ssp. *islandica* from the Barents Sea coast of Norway, Laane (1966) reported n=9, $2n$=18, and regular bivalent formation in pollen mother cells. After field work in Iceland and the Faeroes in 1968 and 1969, Gorenflot (1970) reported n=9, $2n$=18, for plants from eight different localities, including Faxafloi Bay, the site of the collections originally investigated by Löve and Löve (1947). He studied several plants from each locality and in all of them observed only regular bivalent formation. In 1969 Dr. Sturla Fridriksson and Dr. Eythor Einarsson sent me seeds from two Icelandic populations; acetocarmine-squash preparations of buds from growth-chamber plants of these collections showed n=9 (Plate 3; Mrs. Lily Rüdenberg very kindly provided the photomicrograph of collection 107, as well as that of collection 58 of *C. constricta*). Therefore, the bulk of the evidence supports the diploid nature of the Icelandic sea rockets and emphasizes the chromosomal homogeneity of the genus *Cakile*. The tetraploid count was either an error or was based on aberrant plants; if the latter, the research by Gorenflot (1970) suggests that these would be rare. A number of cytotaxonomists have proposed the concept of a disproportionate representation of polyploids in the floras of northern latitudes; the temptation to exemplify this situation with the sea rockets will have to be resisted.

Most of the taxa of *Cakile* have been investigated cytologically, and counts deviating from n=9, $2n$=18, are highly unlikely. It would be reassuring, however, to have counts for at least one additional taxon: *C. arabica*. This is the only inland species of *Cakile*, and peculiarities of morphology and distribution set it apart within the genus. Pobedimova (1963) considered it primitive, a conclusion with which I agree.

The chromosomal data offer little basis for deciding the tribal affinities of *Cakile*. Following Schulz's (1923) hypothesis of a relationship with

TABLE 12. CHROMOSOME NUMBERS IN THE GENUS CAKILE

Species	Chromosome Number	Locality	Reference
C. arctica	n=18, 2n=36	Iceland: Faxafloi Bay (voucher?)	Löve & Löve 1947 (as *C. edentula* ssp. *typica*)
	n=9, 2n=18	Norway: Finnmark (voucher?)	Laane 1966 (as *C. edentula* ssp. *islandica*)
	n=9, 2n=18	Iceland: 7 localities (voucher?)	Gorenflot 1970 (as *C. edentula* ssp. *islandica*)
	n=9, 2n=18	Faeroes: Sandoy (voucher?)	Gorenflot 1970 (as *C. edentula* ssp. *islandica*)
	n=9	Iceland: Vik (Rodman 105, GH)	Rodman
	n=9	Iceland: Seltjarnarnes (Rodman 107, GH)	Rüdenberg (personal communication)
C. constricta	2n=18	Florida: Franklin Co. (Rodman 58, GH)	Rüdenberg (personal communication)
C. edentula ssp. edentula var. edentula	2n=18	California: Sonoma Co. (Kruckeberg 1656, UC)	Kruckeberg 1948
	2n=18	Quebec: Rimouski Co. (Basset & Crompton 4266, DAO)	Mulligan 1964
	2n=18	British Columbia: Clayoquot Island (Calder & Mackay 31959, DAO)	Mulligan 1964
	2n=18	British Columbia: Vancouver Island (Calder & Mackay 31917, DAO)	Mulligan 1964
	2n=18	British Columbia: Queen Charlotte Islands (Calder & Taylor 35336, DAO)	Taylor & Mulligan 1968
C. edentula ssp. edentula var. lacustris	2n=18	Ontario: Elgin Co. (Gillett 10723, DAO)	Mulligan 1964 (as *C. edentula*)
C. edentula ssp. Harperi	2n=18	Florida: Duval Co. (Rodman 24, GH)	Rollins & Rüdenberg 1971
C. geniculata	n=9	Texas: Galveston (Rüdenberg s.n., GH)	Rollins 1966
C. lanceolata ssp. fusiformis	2n=18	Florida: Monroe Co. (Wood 9138, GH)	Rollins & Rüdenberg 1971
C. lanceolata ssp. lanceolata	2n=18	Virgin Islands: St. Johns (Rollins s.n., GH)	Rollins & Rüdenberg 1971
C. lanceolata ssp. pseudoconstricta	n=9	Texas: Aransas Co. (Rollins & Correll 5964, GH)	Rollins 1966 (as *C. fusiformis*)
C. maritima ssp. baltica	n=9	Germany: Kiel (voucher?)	Jaretzky 1929 (as *C. maritima*)
	n=9	Germany: Kiel (voucher?)	Wulff 1937 (as *C. maritima*)

TABLE 12. CHROMOSOME NUMBERS IN THE GENUS CAKILE

Species	Chromosome Number	Locality	Reference
	n=9, 2n=18	Sweden: ? (voucher?)	Löve & Löve 1947 (as *C. maritima*)
	2n=18	Poland: Kuznica (voucher?)	Skalinska *et al.* 1961 (as *C. maritima*)
C. maritima ssp. euxina	2n=18	USSR: Crimea (voucher?)	Pobedimova 1963 (as *C. euxina*)
	2n=18	USSR: ? (voucher?)	Fedorov *et al.* 1969 (as *C. euxina*)
C. maritima ssp. maritima	2n=18	England: Kew (cultivated)	Manton 1932
	n=9	California: San Luis Obispo Co. (Bell 17619, NCU)	Bell 1965
	n=9	France: ? (voucher?)	Delay 1967
	n=9	British Columbia: Queen Charlotte Islands (Calder & Taylor 35430, DAO)	Taylor & Mulligan 1968
	n=9	California: Los Angeles Co. (Shive 68008, Fresno State College Herb.)	Shive 1969
	2n=18	Albania: Durrës (Strid 0506, LD)	Strid 1971

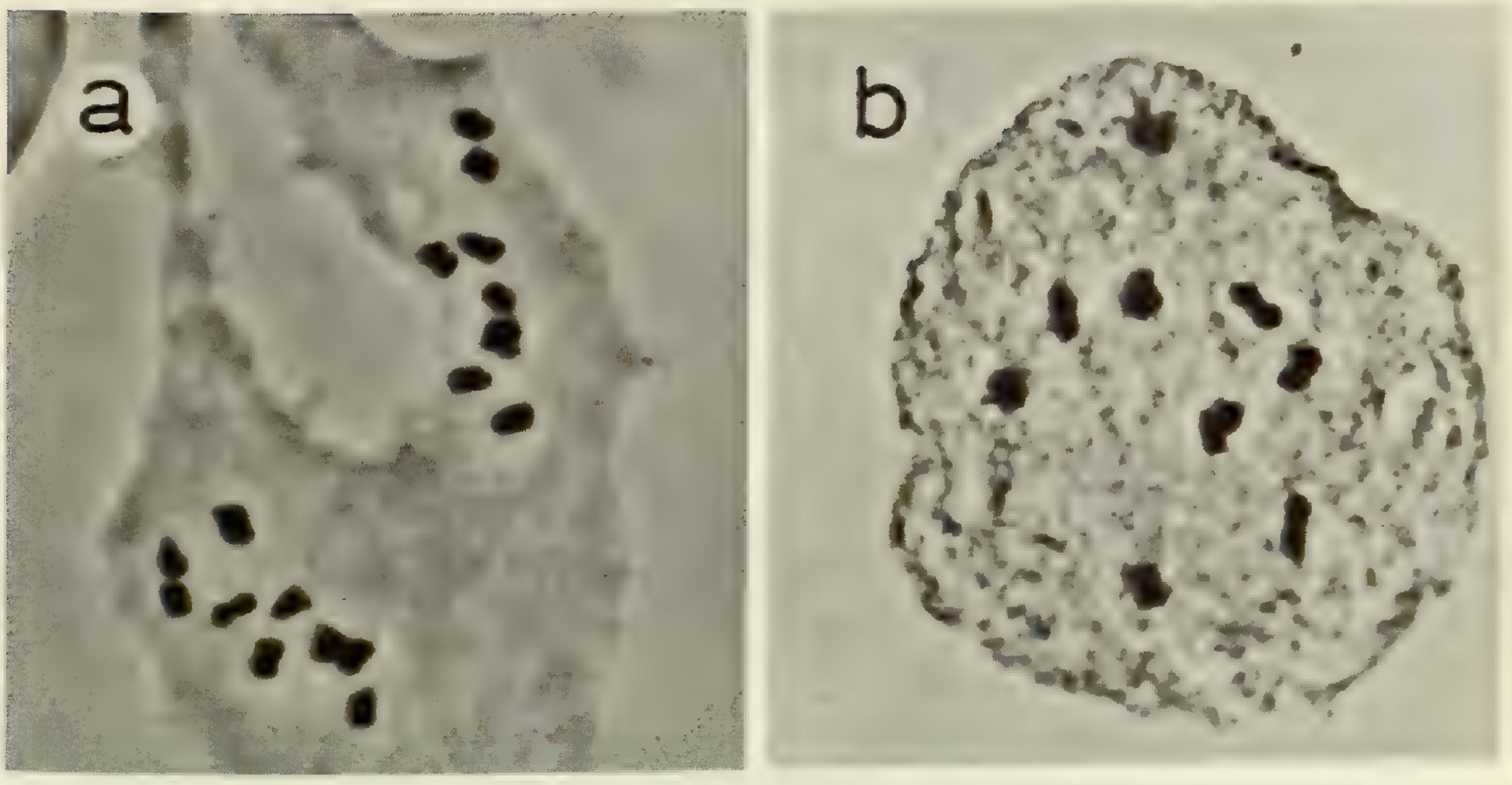


PLATE 3. Photomicrographs of chromosome preparations of *Cakile*. Fig. A. Metaphase II (n=9) in collection 107 of *C. arctica* from Iceland; Fig. B. Metaphase II (n=9) in collection 58 of *C. constricta* from Franklin Co., Florida (photos courtesy of Mrs. Lily Rüdenberg).

Erucaria, Jaretzky (1932) pointed out that the two genera differed in chromosome number, with n=8 for *E. aleppica*, the one species then known cytologically in that genus. Subsequent studies of other *Erucaria* taxa have revealed n-8 as the consistent count (Fedorov *et al.* 1969; Harberd 1972). Manton (1932) assumed that natural subtribal groupings were reflected in uniform base chromosome numbers and criticized taxonomists who related *Cakile* to genera possessing other than n=9. Many of the subtribes of the Cruciferae, however, regardless of whose system is used, are cytologically heterogeneous, as are many genera. The determination of a base number is often difficult if not impossible. In many instances, it would require prior knowledge of the phylogeny of the group to determine the basic condition; yet it is precisely a phylogenetic classification which is the goal of synthesizing the chromosomal data. The inescapable conclusion is that chromosome counts alone cannot provide the criteria for classification of the genera into subtribes or tribes. Chromosomally, the genus *Cakile* rests comfortably within the tribe Brassiceae where it is perhaps most closely associated with the genera of the subtribe Raphanineae (Harberd 1972) with which it shares several morphological features of the fruits (Rytz 1936).

Recently, Kondo (1972) reported the count of n=9 for *Cakile harperi* collected in Pinellas County, Florida, on the Gulf of Mexico. This station is outside the known range of the taxon (treated here as *C. edentula* ssp. *Harperi*) which is confined to the Atlantic Coast of North America. Plants of *C. constricta*, which are somewhat similar vegetatively, may have been confused with this. Not having seen his voucher specimen (*Kondo & Aregood 865*, NCU) to make a determination, I have not included this count in Table 12. Kondo (1972) also remarked that: "[t]his number and previous counts in Darlington and Wylie indicate *Cakile* usually has polyploidy." Such an assessment is not supported by the information assembled here.

Biochemical Systematics

The glucosinolate analyses reported here constitute the first broad chemotaxonomic investigation of the genus *Cakile*. Sea rockets have been analyzed previously, however, usually during the course of extensive chemical surveys, and the literature on natural products yields a number of reports on the presence of various compounds. These include alkaloids in the leaves of *C. maritima* (Aplin & Cannon 1971), protein and non-protein amino acids in the seeds of *C. edentula* (Miller *et al.* 1962; Larsen 1969), seed oil fatty acids (Mikolajczak *et al.* 1961; Miller *et al.* 1965; Appelqvist 1971), and glucosinolates. The absence of particular classes of natural products has also been reported. Earle and Jones (1962), for example, obtained negative results from tests for starch, alkaloids, and tannins on seeds of *C. edentula*, and Vaughan and

Whitehouse (1971) reported finding no mucilage in the seeds of *C. endentula* and *C. maritima.*

The composition of fatty acids in seed lipids has been shown by Barclay, Gentry and Jones (1962) to be taxonomically useful in the genus *Lesquerella*, and the available data suggest that this class of compounds may also prove important in *Cakile.* Table 13 has been constructed from data on *C. edentula* (Mikolajczak *et al.* 1961) and

TABLE 13. FATTY ACID COMPOSITION OF SEEDS OF CAKILE EDENTULA AND C. MARITIMA (AREA PERCENTAGE BY GAS-LIQUID CHROMATOGRAPHY.)

	14:0	16:0	16:1	18:0	18:1	18:2	18:3	20:0	20:1	20:2	20:3	22:0	22:1	22:2	22:3	24:1
C. edentula[1]	0	4	0.2	2	23	26	18	1	7	0.6	0	1	17	t	t	0
C. maritima[2]	?	6	?	2	17	19	16	1	5	0	?	5	26	?	?	1
C. maritima[3]	?	6	?	1	14	21	27	?	7	?	?	?	21	?	?	0.2
C. maritima[3]	?	6	?	1.5	17	18	27	?	8	?	?	?	21.5	?	?	0.3
C. maritima[3]	?	7	?	1	14	18	26	?	8	?	?	?	25	?	?	0.4
C. maritima[3]	?	6	?	2	14	19	20	?	8	?	?	?	26	?	?	0.6

Legend: 1. Mikolajczak *et al.* 1961. 2. Miller *et al.* 1965. 3. Appleqvist 1971. t. Trace amounts present. ?. Not specifically reported.

C. maritima (Miller *et al.* 1965; Appelqvist 1971) for which similar methods of analysis were employed (gas chromatography of the fatty acid methyl esters following methanolysis of the seed lipids). The seeds of *Cakile* proved particularly rich in oil; it comprised 49% on a dry weight basis of *C. edentula* seed and 44% of *C. maritima* seed (Mikolajczak *et al.* 1961 and Miller *et al.* 1965, respectively), values which were among the highest found in these surveys. It is evident from Table 13 that the two species are qualitatively very similar but differ quantitatively for a number of constituents. In particular, the differences between the two in percentage composition of oleic (18:1), linoleic (18:2), behenic (22:0), and erucic (22:1) acids may be significant. In a study of the variation in percentage composition of fatty acids in *Crambe abyssinica, Eruca sativa,* and *Raphanus sativus* Mikolajczak *et al.* (1961) reported a range of variation of three percent for erucic acid within a species and concluded that for fatty acids in general there was little variation within a species. Differences within *Cakile maritima* of nine percent for linolenic acid (18:3) and of five percent for erucic acid are evident from Table 13, however. These differences may be taxonomic since the sample of *C. maritima* analyzed by Miller *et al.* (1965) originated from the coast of Israel (Dr. Arthur Barclay, personal communication) and is most likely *C. maritima* ssp. *maritima* while the four samples analyzed by Appelqvist (1971) were obtained in Sweden and are most likely *C. maritima* ssp. *baltica.* The sample of *C. edentula* analyzed by Mikolajczak *et al.* (1961) was collected from the coast of Virginia near Norfolk (Dr. Barclay, personal communication).

Mustard oil glucosides (glucosinolates, Fig. 1) constitute a second class of natural products of potential taxonomic utility. Over 60 of these unique compounds are known (Ettlinger & Kjær 1968; Elliott & Stowe 1970; Gmelin, Kjær & Schuster 1970; Kjær & Schuster 1970, 1971, 1972; Kjær & Wagnières 1971; Underhill & Kirkland 1972), and most can be readily isolated, separated, and identified by combined paper and gas chromatography. Their application to taxonomic problems was initiated by Kjær and Hansen (1958) in a paper-chromatographic analysis of four species of *Arabis*. Studies of the genus *Brassica* (Ettlinger & Thompson 1962; Josefsson 1970) demonstrated a generally characteristic pattern of glucosinolates in recognized taxa although considerable variation was found among the many cultivars of this genus. It was to assess the usefulness of glucosinolates for systematic purposes in the genus *Cakile* that I understook an extensive paper- and gas-chromatographic analysis of field collections from North America and the West Indies as well as of seed samples from Australia, Iceland, Norway, and Denmark.

Two extensive, complementary reviews on glucosinolates have been published (Kjær 1960; Ettlinger & Kjær 1968). These provide an excellent historical account of the development of our knowledge of these unique plant constituents and much information on chemical and botanical aspects of the compounds. The more recent review includes a chemical classification of the 50 glucosinolates then known and a critical appraisal of the distribution of these thioglucosides in the plant kingdom.

Probably the first report of a particular mustard oil from *Cakile* was made by the botanist James Wright (1927) who observed ". . . the characteristic odour of Allyl isothiocyanate . . ." after applying a solution of myrosinase to histological sections of *C. maritima*. Kjær, Conti, and Larsen (1953), using the new technique of paper chromatography of the thiourea derivatives, reported isolating only a single compound, allylthiourea, from seeds of this species. Danielak and Borkowski (1969)

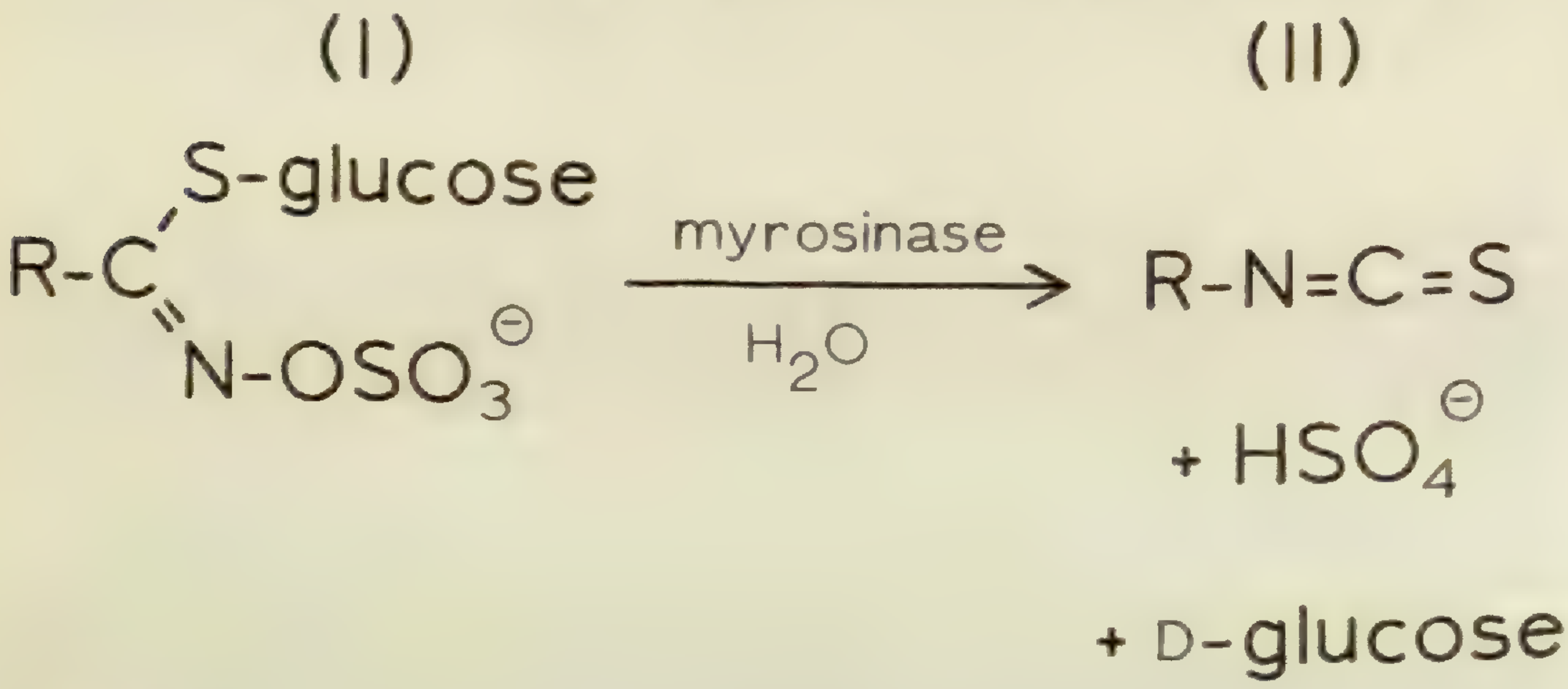


FIG. 1. General reaction for the enzymatic hydrolysis of glucosinolates (I) to isothiocyanates (II).

likewise reported finding only this one compound in their studies on seeds of *C. maritima*. By paper-chromatographic analysis of the unripe fruits, Delaveau (1957) detected seven compounds in *C. maritima*, four of which he tentatively identified as allyl, 3-butenyl, 4-pentenyl, and phenylethyl isothiocyanates. Daxenbichler *et al.* (1964), analyzing seeds of *C. edentula*, reported allyl and *sec*-butyl thioureas as well as a third, unidentified compound. Results from a paper-chromatographic analysis of two samples of *Cakile*, done previously by Dr. Martin Ettlinger, who was an Honorary Research Associate in the Gray Herbarium 1969–70, demonstrated two distinct patterns of glucosinolate composition. These results encouraged a belief in the systematic value of the compounds in this genus which my investigations have subsequently confirmed.

Material and Methods. Seeds from mature (i.e., dry and corky) fruits were used for all the analyses, both by paper and gas chromatography. The fruits were stored at room temperature in paper packets for up to three years or, in a few cases, in a refrigerator at 5° C. for one year and shelled just prior to analysis. The different storage conditions did not appear to affect the glucosinolate composition of the seeds. Appendix I gives the identity and place of collection of all the samples analyzed. Whenever possible, mass samples were analyzed, that is, samples of seeds collected from 25 to 60 (usually 50) plants in a local area. In such instances, the seeds originate from one of the four lowermost mature fruits on the main or central raceme of the plant. When seeds from a single plant or only a few plants were analyzed, mature fruits from the entire length of a raceme were used.

For the analysis by paper chromatography, the glucosinolates are not chromatographed directly; rather, the seeds are treated with a preparation of the myrosinase enzyme to yield isothiocyanates which are then treated with ammonia to produce thioureas. It is the resulting thioureas which are chromatographed in up to six different solvent systems, and the spots, developed by spraying with Grote's reagent, are then identified by their mobilities relative to that of a reference compound, phenylthiourea. Separate tests are run to detect the presence of *p*-hydroxybenzyl isothiocyanate and oxazolidine-2-thiones. The detailed procedure has been described previously (Kjær & Rubinstein 1953; Ettlinger & Thompson 1962; Ettlinger *et al.* 1966). The six solvent systems employed were: n-butyl alcohol, toluene, and water, 3:1:1 ("butanol" solvent); toluene, n-butyl alcohol, and water, 3:1:2 ("3 toluene" solvent); toluene, n-butyl alcohol, and water, 10:1:2 ("10 toluene" solvent); toluene, acetic acid, and water, 5:2:4 ("toluene-acetic" solvent); benzene, ethanol, and water, 5:1:2 ("benzene" solvent); and chloroform and water, 5:3 ("chloroform" solvent). The distance in centimeters of the center of a spot from the starting point on a chromatographic strip was measured, and this number, divided by the distance traveled by the

reference compound, phenylthiourea, gave an "R_{Ph}" value which characterizes the mobility of that particular compound in that solvent. Occasionally, a compound can be identified from its R_{Ph}-value in a single solvent system; allylthiourea, for example, has an R_{Ph} of 0.25 ± 0.05 in the chloroform solvent which appears to be unique. More often, the pattern of mobilities in more than one solvent must be used to identify a compound. While this paper-chromatographic procedure does not discriminate all known glucosinolates, it serves to identify with reasonable accuracy a majority of the glucosinolates found thus far in higher plants.

The technique of gas chromatography for the analysis of glucosinolates was first reported by Kjær and Jart (1957) and by Jart (1961), who chromatographed the enzymatically released isothiocyanates. Subsequent reports on gas chromotography of isothiocyanates confirmed its great utility for quantification of the compounds (Youngs & Wetter 1967) and for discrimination of complex mixtures (Binder 1969).

Seeds, 0.1 to 1.2 g, were ground with a mortar and pestle, transferred to a 250 ml Erlenmeyer flask, and overlaid with 100 ml of anhydrous ethyl ether, free of alcohols and peroxides. The flasks were left in the dark at room temperature for three to five hours with occasional shaking. The defatted seed meal was then filtered off, washed with ether, air-dried a few minutes, and transferred to a 50 ml Erlenmeyer flask. To this were added 7–10 ml of ethyl ether, 5 ml of distilled water, 0.1 ml of ascorbate solution, and two drops of the myrosinase preparation (Ettlinger & Thompson 1962). The flasks were placed on a mechanical shaker, operated slowly, and left overnight in the dark at room temperature. In the morning the ether solution was pipetted into 10 ml volumetric flasks, which could be stored in a refrigerator. A variant of this procedure was used after it was noticed that spurious compounds were appearing on chromatograms as a probable result of some endogenous enzymatic activity. To the ether-extracted seed meal, before addition of the myrosinase, boiling 70% methanol was added, and the mixture was left to boil for 15 minutes, by which time the methanol had evaporated leaving an aqueous mixture. After cooling, the ascorbate solution and myrosinase were added, and the procedure was continued as outlined above. The technique effectively eliminated these spurious compounds, probably by destroying all native enzymatic activity.

The ether solutions of isothiocyanates were chromatographed on an F & M Model 402 gas chromatograph with a hydrogen flame ionization detector, linked to a Hewlett-Packard Model 7127A strip chart recorder and operated isothermally at 80° C. (flash heater 130° C. and flame detector 145° C.) and at 160° C. (flash heater 200° C. and flame detector 170°C.). A single glass U-column, 6 ft × 3 mm I.D., packed with 6% DC–560 plus 2% EGSP–Z on 100/120 Gas Chrom Q (from Applied Science Laboratories, State College, Pa. 16801), was employed, with helium as the carrier gas at an approximate flow rate of 60 cc/min. The

size of the injected sample varied from one to five microliters. For quantitative comparison, peak areas on the chromatograms were computed by height × width at half-height. There was no difficulty with overlapping compounds in the two runs, at 80° C. and at 160° C., since all peaks appearing within the first 13 minutes at 80° C. came off in less than one minute at 160° and were usually obscured by the ether. No attempt was made to quantify absolutely the glucosinolate content of the seeds; only relative amounts of the isothiocyanates appearing on the chromatograms were determined. Identification of the peaks was made by judicious comparison with the results from the paper-chromatographic analyses of the same sample and by comparison with gas chromatograms of synthetic isothiocyanates or extracts from species known to possess particular glucosinolates. In questionable cases, the sample and the suspected isothiocyanate (synthetic or derived from a known plant source) were mixed together and chromatographed, and complete overlap of the peaks was assumed to indicate identity of these compounds.

Twenty-one enzymatic products were detected by paper and gas

TABLE 14. GLUCOSINOLATE HYDROLYSIS PRODUCTS FROM SEEDS OF CAKILE.

Compound Number	Name	R (Fig. 1)	Retention time in min. @80°C.
1	unknown 1	?	1.6– 1.7
2	isopropyl[a]	$(CH_3)_2CH$	2.0– 2.2
3	allyl[a]	$CH_2=CHCH_2$	2.8– 3.1
4	*sec*-butyl[a]	$C_2H_5CH(CH_3)$	3.5– 3.9
5	3-butenyl[a]	$CH_2=CH(CH_2)_2$	5.3– 6.1
6	unknown 2	?	7.8– 9.4
7	4-pentenyl[a]	$CH_2=CH(CH_2)_3$	10.0–11.5
			Retention time in min. @160°C.
8	unknown 3	?	1.3– 1.4
9	unknown 4	?	1.6– 1.7
10	unknown 5	?	1.9– 2.2
11	3-methylthiopropyl[a]	$CH_3S(CH_2)_3$	2.7– 3.1
12	unknown 6	?	2.9– 3.5
13	benzyl[a]	$C_6H_5CH_2$	3.5– 3.9
14	4-methylthiobutyl[a]	$CH_3S(CH_2)_4$	4.5– 5.4
15	2-phenylethyl[a]	$C_6H_5(CH_2)_2$	5.6– 6.5
16	5-methylthiopentyl[a]	$CH_3S(CH_2)_5$	7.3– 8.6
17	6-methylthiohexyl[a]	$CH_3S(CH_2)_6$	11.5–12.4
			R_{Ph} in "Butanol" solvent
18	3-methylsulfinylpropyl[b]	$CH_3SO(CH_2)_3$	0.37
19	4-methylsulfinylbutyl[b]	$CH_3SO(CH_2)_4$	0.43
20	5-methylsulfinylpentyl[b]	$CH_3SO(CH_2)_5$	0.58
21	4-methylsulfonylbutyl[b]	$CH_3SO_2(CH_2)_4$	0.52

a = isothiocyanate; b = thiourea.

chromatography following treatment of the seed meals of *Cakile* with myrosinase, and 15 of the presumed parent glucosinolates have been identified chemically (Table 14). The procedure for identification —involving comparison by paper chromatography of sample R_{Ph} values with a table of the known mobilities of 42 thioureas and oxazolidine-2-thiones (Dr. Martin Ettlinger, unpublished results) and comparison by gas chromatography of sample retention times with the retention times of synthetic isothiocyanates or of extracts from plants known to yield a particular mustard oil—is reasonably accurate and discriminating though not conclusive. The paper-chromatographic procedure does not discriminate, for example, isobutyl and *sec*-butyl glucosinolates (Ettlinger & Kjær 1968) although there is evidence that gas chromatography does distinguish the two (Binder 1969; Dr. Ihsan Al-Shehbaz, personal communication). Such a caveat applies to all chromatographic analyses. Absolute identification of the constituents would require spectroscopic studies and even chemical syntheses, which a taxonomist usually cannot undertake. The 21 glucosinolate hydrolysis products are listed in Table 14 with their gas-chromatographic retention times at 80° C., 160° C. or the R_{Ph} values in butanol solvent. Neither *p*-hydoxybenzyl isothiocyanates nor oxazolidine-2-thiones were encountered in the tests for these, and the corresponding glucosinolates are presumably absent from seeds of *Cakile*.

No effort was made to analyze other plant parts for glucosinolates except for collection 107 from Iceland, for which fresh leaves of greenhouse-grown plants were analyzed by paper chromatography in chloroform solvent. One compound, allylthiourea, was detected, which corresponds to the major constituent of seeds of this collection. It should not be expected, however, that the same glucosinolates will be found in other parts of the same plant. Working with species of *Brassica* and with *Sinapis alba*, researchers have reported significant differences in glucosinolate composition in different plant parts (Josefsson 1967, 1970; Bergman 1970; Kondra & Downey 1970). Moreover, developmental differences in glucosinolate composition have been demonstrated in various plant organs (Kondra & Downey 1969; Bergman 1970; Tang 1971). The use of mature seeds in this study of *Cakile* eliminates these sources of variation.

Table 15 presents the results of paper-chromatographic analyses of 27 seed samples from 21 populations of *Cakile* along with the unpublished results from two analyses (M. G. Ettlinger and C. P. Thompson, personal communication) on *C. maritima* ssp. *maritima* from California (no voucher) and *C. geniculata* from Tamaulipas, Mexico (voucher: *Johnston* 2547, GH). An estimate of the quantitative relationships in each sample was made on the basis of the size and intensity of color of the spots after spraying with Grote's reagent, and each compound was classified as either primary (P) or secondary (S). Secondary compounds include

TABLE 15. GLUCOSINOLATE COMPOSITION OF SEEDS OF CAKILE DETERMINED BY PAPER CHROMATOGRAPHY OF THE THIOUREA DERIVATIVES.

Sample	Compound (see Table 14) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
94a/L			P	S	S						S										
94b		P		P							S			S				S			
103/U		S	P	P																	
104/U		S	P	P																	
95/U		S	P	S	S						S										
95/L		S	P	S	S						S										
95/U			P	S	S						S										
95/L			P	S	S						S										
100/L			P	S	S						S										
98/L		S	P	S	S						S										
97/L		S	P	S	S						S										
99/L		S	P	S	S						S										
96/L		S	P	S	S						S										
96/L		S	P	S	S						S										
39/L			P	S	S						S							?			
41/U			P		P								S				?				
43			S		P	?							S		S		?				
44			S		P	?							S		S						
45/L			S		P								S		S		S		?		
48			S		P								S		S		S		?		
50			S	S	P								S				?				
52			S		P								S		S						
53			S		P								S		S						
65b/L			S		P						S		S								
65a/L			P		P						S		S								
R-s.n.-2/L					P																
B-103/L			S		P	?					S		S		S						
C. mar.		P		P							S		S		S	S	S	S	S		
C. gen.			P		P						S		S								

Legend: P, primary compound; S, secondary or trace compound.

those appearing as only trace spots on a few chromatograms. The results of the gas-chromatographic analyses of 96 seed samples are presented in Table 16. Tracings of gas chromatograms of four samples are shown in Figures 2–5. The taxonomic identity of the collections, locality, date of collection, and voucher are given in Appendix I.

Of the 27 samples which I analyzed by paper chromatography, all but two (collection 94b from Oregon and R-s.n.–2 from St. John, Virgin Islands) were also analyzed by gas chromatography. With some of these samples, however, lower seeds (that is, seeds from the lower fruit segment) were used in the one type of analysis and upper seeds in the other, or lower or upper seeds were used in one and a mixture of both in the other type of analysis (a mixture being indicated by the absence of "/L" or "/U" after the collection number in Tables 15 and 16). One obvious

TABLE 16. VOLATILE ISOTHIOCYANATE COMPOSITION OF SEEDS OF CAKILE AS DETERMINED BY GAS CHROMATOGRAPHY (PEAK-AREA PERCENTAGE BY TRIANGULATION)

Sample	R Unknown 1	$(CH_3)_2CH$	$CH_2{=}CHCH_2$	$C_2H_5CH(CH_3)$	$CH_2{=}CH(CH_2)_2$	Unknown 2	$CH_2{=}CH(CH_2)_3$	Unknown 3	Unknown 4	Unknown 5	$CH_3S(CH_2)_3$	Unknown 6	$C_6H_5CH_2$	$CH_3S(CH_2)_4$	$C_6H_5(CH_2)_2$	$CH_3S(CH_2)_5$	$CH_3S(CH_2)_6$
Australia																	
*P-s.n.	0	18.3	5.5	60.5	4.4	0	0	0	0	T	1.5	0	0	7.9	0	2.0	0
Pacific Coast																	
*28-2/U	0	1.7	37.2	60.8	T	0	0	0	0	0	T	0	0	0	0	0	0
*91	0	1.1	62.6	35.6	T	0	0	0	T	T	T	0	T	0	0	0	0
90	0	20.0	T	38.6	0	0	0	2.1	0	T	22.3	0	0	12.1	0	4.1	0
89	0	T	89.2	7.6	1.1	T	0	0	T	0	1.4	0	0.3	0	0	0	0
94a/U	0	T	94.8	2.0	1.0	0	0	0	T	0	1.8	0	0.3	0	0	0	0
*87	0	21.7	0	46.5	0	0	0	T	0	T	T	1.5	0	12.0	0	15.3	1.4
*82	0	14.6	T	63.2	0	0	0	T	0	T	11.5	0	0	6.7	0	2.8	0
*79	0	16.0	T	49.9	T	0	0	T	0	T	17.4	0	0	10.6	0	4.1	T
*76	0	17.3	1.3	48.4	1.1	0	0	T	0	T	21.2	0	0	7.0	0	2.8	0
73	0	P	P	P	0	0	0	0	0	P	P	0	0	P	0	P	0
*71	0	7.0	T	72.0	T	0	0	T	0	T	10.3	0	0	7.0	0	2.9	T
69	0	32.7	T	34.0	0	0	0	3.5	0	1.8	12.2	0	0	10.0	0	5.4	T
Great Lakes																	
102-2/U	0	T	94.4	4.1	1.1	T	0	0	T	0	T	0	T	T	0	0	0
132	0	0	94.2	4.4	1.0	0	0	0	T	0	T	0	0	0	0	0	0
133	0	T	93.2	4.8	0.8	0	0	0	T	0	0.9	0	T	0	0	T	0
*27-2/U	0	0	94.5	1.9	0.6	0	0	0	T	0	3.0	0	0	0	0	0	0
Atlantic Coast of North America																	
*31-2/U	0	1.2	39.5	59.0	T	0	0	0	0	0	T	0	0	0	0	0	0
137/L	0	1.2	55.0	40.0	1.8	0	0	0	0	0	1.8	0	0.1	0	0	0	0
136/L	0	T	92.0	3.4	1.8	0	0	0	T	0	1.8	0	0.8	0	0	0	0
103	0	3.2	45.5	50.8	T	0	0	0	T	0	1.2	0	T	0	0	0	0
*34-2/U	0	1.0	45.6	53.1	T	0	0	0	0	0	T	0	0	0	0	0	0
104	0	2.7	47.9	48.2	0.6	0	0	0	T	0	0.6	0	T	0	0	0	0
*95/L	0	T	96.1	2.3	0.6	0	0	0	T	0	0.6	0	0.3	0	0	0	0
95	0	T	85.1	11.6	1.4	T	0	0	T	0	1.5	0	T	0	0	0	0
26/L	0	T	89.1	8.5	0.7	0.9	0	0	T	0	T	0	T	0	0	0	0
26-2/L	0	T	89.8	6.0	0.8	0.4	0	0	T	0	2.8	0	0.2	0	0	0	0
151/L	0	0	91.4	4.1	1.6	1.2	0	0	T	0	1.3	0	T	0	0	0	0
150/L	0	0	88.4	6.2	1.3	2.2	0	0	T	0	1.2	0	0.7	0	0	0	0
100/L	0	T	96.2	2.6	0.6	T	0	0	T	0	T	0	0	0	0	0	0

Legend: R = variable side-chain; cf. Fig. 1. T = trace amounts present. P = present but not quantified./L = seeds from only lower fruit segments used./U = seeds from only upper fruit segments used. ° = extracted in boiling 70% methanol. **Boldface = mass sample analyzed.**

Sample	R Unknown 1	$(CH_3)_2CH$	$CH_2{=}CHCH_2$	$C_2H_5CH(CH_3)$	$CH_2{=}CH(CH_2)_2$	Unknown 2	$CH_2{=}CH(CH_2)_3$	Unknown 3	Unknown 4	Unknown 5	$CH_3S(CH_2)_3$	Unknown 6	$C_6H_5CH_2$	$CH_3S(CH_2)_4$	$C_6H_5(CH_2)_2$	$CH_3S(CH_2)_5$	$CH_3S(CH_2)_6$
Atlantic Coast of North America (cont.)																	
98/L	0	T	90.3	8.7	0.9	0	0	0	0	0	T	0	0	0	0	0	0
97/L	0	T	91.3	7.1	1.1	T	0	0	T	0	0.5	0	0	0	0	0	0
99/L	0	T	87.0	11.1	1.1	0	0	0	T	0	0.7	0	T	0	0	0	0
96/U	0	T	91.0	5.9	0.9	0	0	0	T	0	1.9	0	T	0	0	0	0
96/L	0	T	85.9	10.8	1.6	0	0	0	T	0	1.5	0	T	0	0	0	0
96-2/L	0	T	95.8	3.5	0.6	0	0	0	0	0	T	0	T	0	0	0	0
39/U	0	0	89.2	4.8	1.9	0	0	0	T	0	3.4	0	T	0	0	0	0
40	0	0	82.3	4.0	12.5	0	0	0	T	T	T	0	0.6	0	0	0	0
41	4.0	0	25.1	T	68.0	0	0.8	T	T	0	T	T	0	0.8	T	T	0
43	9.9	0	3.2	0.3	77.9	0	4.1	T	T	T	0.7	T	0	1.6	0.5	1.1	0
44	8.2	0	3.0	0.3	83.4	0	1.9	T	T	T	0.6	T	0	1.1	T	0.8	0
*45/U	5.7	0	3.0	T	90.3	0	0.7	T	T	T	T	T	0	T	T	T	0
*45/L	5.3	0	2.8	0.4	90.3	0	0.5	T	T	T	0	0	0	T	T	T	0
45	7.8	0	3.2	0.5	85.1	0	0.6	T	T	T	0.6	T	0	0.8	T	0.6	0
24-3	13.4	0	4.4	0.3	78.9	0	1.3	T	T	0	0.6	T	0	T	T	T	0
47/L	7.1	0	3.8	0.3	82.2	0	1.6	T	T	T	T	T	0	2.7	T	1.1	0
131/L	7.3	0	2.9	0.7	86.0	0	1.4	T	T	T	0.5	T	0	T	T	T	0
*131-2	5.3	0	2.6	0.4	89.8	0	0.7	T	T	0	0	0	0	T	T	T	0
48	8.8	0	2.8	0.2	82.5	0	3.1	T	T	T	T	T	0	1.2	T	0.5	0
49/L	2.5	0	7.9	5.6	79.6	0	0	T	0	T	0.8	0	0	3.5	0	0	0
50	9.4	0	6.0	7.3	66.8	0	0	T	0	4.6	0.6	0.6	0	4.1	0	0.3	0
52	9.9	0	8.9	T	73.9	0	T	T	0	1.8	T	T	0	4.1	0	0.6	0
51	9.6	0	6.4	0	78.8	0	T	T	0	0.8	0.7	T	0	3.5	0	T	0
G-7659	8.9	0	8.5	0	63.1	0	0	2.8	0	6.4	2.7	T	0	7.2	0	T	0
W-9138/U	3.4	0	11.6	0	75.3	0	0	0	0	0.6	2.8	0	0	5.6	0	0.6	0
W-9138-2	8.6	0	9.2	0	76.3	0	0	T	0	1.0	1.1	T	0	3.6	0	T	0
55	3.3	0	6.8	T	85.5	0	0	T	0	T	0.9	0	0	2.8	0	T	0
53	7.6	0	8.5	0	76.2	0	0	T	0	1.2	0.8	T	0	5.3	0	T	0
Gulf of Mexico																	
56	1.8	0	5.5	T	89.8	0	0	T	0	T	0.4	0	0	2.0	0	T	0
130/L	1.0	0	10.9	0	85.3	0	0	0	0	0	0.8	0	0	2.0	0	T	0
57	4.5	0	23.9	0	65.8	0	0	1.2	0	1.0	1.4	0	0	2.3	0	T	0
58	1.9	0	11.6	0	85.8	0	0	0	0	T	0.2	0	0	0.5	0	0	0
60	6.7	0	12.1	4.5	69.9	0	0	T	0	2.4	0.6	T	0	2.8	0	0	0
62	4.7	0	16.6	1.5	73.6	0	0	T	0	0.7	0.6	T	0	2.4	0	0	0
62 "P_1"	1.7	0	18.4	T	79.3	0	0	T	0	0	T	0	0	T	0	T	0
62 "H"	3.9	0	9.1	0	83.8	0	0	T	0	T	0.6	T	0	1.6	0	T	0
62 "P_2"	5.5	0	11.4	0	69.9	0	0	3.6	0	2.1	1.5	T	0	5.2	0	T	0
63a	5.5	0	29.0	T	63.0	0	0	T	0	T	1.1	0	0	0.8	0	0	0
25-3	6.7	0	29.4	T	57.0	0	0	1.5	0	T	2.9	0	0	2.2	0	0	0
64	8.2	0	13.3	T	71.5	0	0	2.0	0	1.2	T	T	0	2.4	0	T	0

Sample	R	$CH_3S(CH_2)_3$	Unknown 6	$C_6H_5CH_2$	$CH_3S(CH_2)_4$	$C_6H_5(CH_2)_2$	$CH_3S(CH_2)_5$	$CH_3S(CH_2)_6$
	Unknown 1	Unknown 5						
	$(CH_3)_2CH$							
	$CH_2=CHCH_2$							
	$C_2H_5CH(CH_3)$							
	$CH_2=CH(CH_2)_2$							
	Unknown 2							
	$CH_2=CH(CH_2)_8$							
	Unknown 3							
	Unknown 4							

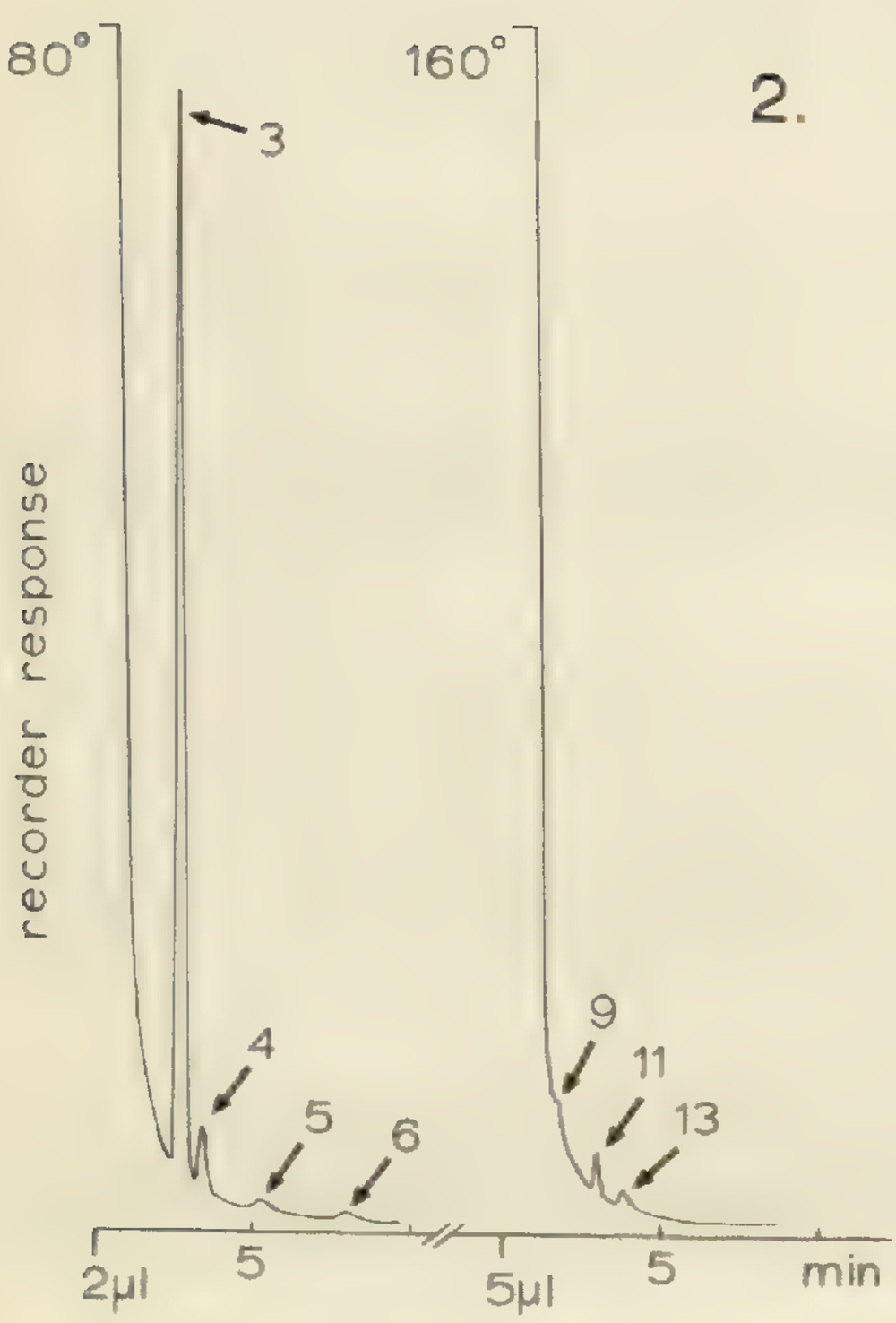
Gulf of Mexico (cont.)

65a	2.1	0	17.6	0	76.3	0	0	1.1	0	T	1.1	0	0	1.4	0	0	0
65b/L	12.9	0	7.3	1.4	70.5	0	0	T	0	3.4	T	T	0	3.1	0	0	0
*66/U	7.4	0	11.4	0	78.9	0	0	T	0	T	T	0	0	2.1	0	0	0
*66/L	7.9	0	12.3	T	77.6	0	0	T	0	T	T	0	0	1.7	0	0	0
66	3.7	0	8.9	T	82.6	0	0	1.3	0	T	T	0	0	2.4	0	0	0
67/L	3.0	0	3.0	0.2	93.6	0	T	T	0	T	T	T	0	T	0	T	0
*129-2	2.5	0	22.3	T	70.8	0	0	T	T	T	2.3	0	0	1.8	0	0	0
*F-41920/U	0	0	0	0	52.7	0	0	0	0	T	0	0	0	47.3	0	0	0
Lesser Antilles																	
R-s.n.-3	2.6	0	0.8	0	95.0	0	T	T	0	T	T	T	0	1.4	0	T	0
Puerto Rico																	
30-2	4.7	0	0.5	0	94.0	0	T	T	0	T	T	0	0	T	0	0	0
Jamaica																	
112	3.7	0	6.0	0	77.0	0	0	T	0	1.5	1.9	0	0	9.8	0	T	0
*114	10.8	0	12.1	0	72.5	0	0	T	T	T	T	0	0	3.4	0	T	0
*116	9.7	0	5.7	0	83.3	0	0	T	0	T	T	0	0	1.2	0	T	0
*117	4.2	0	4.5	0	79.9	0	T	T	0	T	2.4	0	0	8.5	0	T	0
*118	5.7	0	6.9	0	75.3	0	T	T	T	T	2.2	0	0	8.9	0	T	0
119	7.6	0	26.8	0	61.6	0	0	T	0	T	1.0	0	0	2.0	0	0	0
Bahamas																	
B-103	6.0	0	7.8	0.6	76.0	0	0.9	T	0	1.1	1.0	T	0	4.9	0.7	0.6	0
*32/U	2.4	0	1.4	0	77.8	0	T	T	0	T	1.0	0	0	15.5	T	T	0
*33	8.0	0	8.7	0	75.4	0	0	T	0	T	1.4	0	0	5.6	T	T	0
Bermuda																	
127	1.3	0	69.1	27.9	T	0	0	0	0	0	1.2	0	0	0.6	0	0	0
128	2.1	0	55.6	41.2	0.4	0	0	0	0	0	T	0	0	T	0	0	0
Iceland																	
*107-2	0	0	92.2	0	T	T	0	T	T	T	6.4	0	0	T	T	0	0
Northern Europe																	
*29-3	0	1.3	68.4	29.2	1.1	T	0	0	0	0	T	0	0	0	0	0	0
*153	0	T	96.5	3.0	T	T	0	0	0	0	0.5	0	0	0	0	0	0
*154	0	T	92.5	5.3	T	0.5	0	0	0	0	1.4	0	0	0	0	0	0
*152/U	0	T	8.9	91.1	0	0	0	0	0	0	0	0	0	0	0	0	0

difference between the results of the two methods lies in the absence of compounds 18 to 21 from gas chromatograms. These ω-methylsulfinylalkyl (18–20) and ω-methylsulfonylalkyl (21) isothiocyanates have very high boiling points, may not emerge from the column under the conditions of the gas-chromatographic procedure used here, and consequently go undetected. Their absence does not invalidate the comparisons between samples of the quantitative ratios of the remaining compounds detected since it is the relative concentrations within a sample which have been calculated. Furthermore, the paper chromatograms indicate that these glucosinolates, when present, occur in small or trace amounts. Another major difference between the results of the two techniques concerns the eight compounds detected by gas chromatography which were not found on paper chromatograms. These are compounds 1, 6, 8, 9, 10, and 12 (Unknowns 1–6), 13 (benzyl isothiocyanate), and 15 (2-phenylethyl isothiocyanate). All of these were detected in seeds following extraction in boiling methanol; thus, it is unlikely that they are the products of enzymatic activity other than the action of myrosinase on glucosinolates. All except Unknown 1 occur in very small or trace amounts, and their absence from paper chromatograms is therefore understandable. Unknown 1, occurring in much larger amounts, should have been detected on paper chromatograms. It may be one of those compounds which the method does not discriminate or among the unidentified spots with an R_{Ph} value below 0.37 in the "butanol" solvent encountered in a few samples (collections 41, 45, and 48, for example). Work is in progress on elucidating the nature of this compound (Dr. M. G. Ettlinger, personal communication), which has also been found in the genus *Thelypodium* (Dr. Ihsan Al-Shehbaz, personal communication).

A discussion of the taxonomic significance of the results requires a preliminary comment on three specific matters. These concern comparisons between the dimorphic seeds of *Cakile*, between single-plant and mass samples, and between wild plants and those cultivated in the greenhouse or growth chambers (and often inbred).

In regard to the glucosinolate composition of the two morphologically dissimilar seeds in the fruit of *Cakile*, there is no qualitative difference between the two and only slight quantitative differences, if any. In Table 15, for example, analyses of upper and lower seeds from a mass sample and of upper and lower seeds from a single plant of collection 95 (*C. edentula* from Cape Cod, Massachusetts) demonstrate the same qualitative and quantitative pattern. From the gas-chromatographic results in Table 16, which are quantitatively more precise, a comparison between upper and lower seeds of a mass sample of collection 96 (*C. edentula* from Maryland) demonstrates the same qualitative pattern and only slight quantitative differences. Upper and lower seeds from single plants of collections 45 *(C. edentula* ssp. *Harperi)* and 66 *(C. geniculata)* again have a similar glucosinolate composition. The somatic dimorphism of

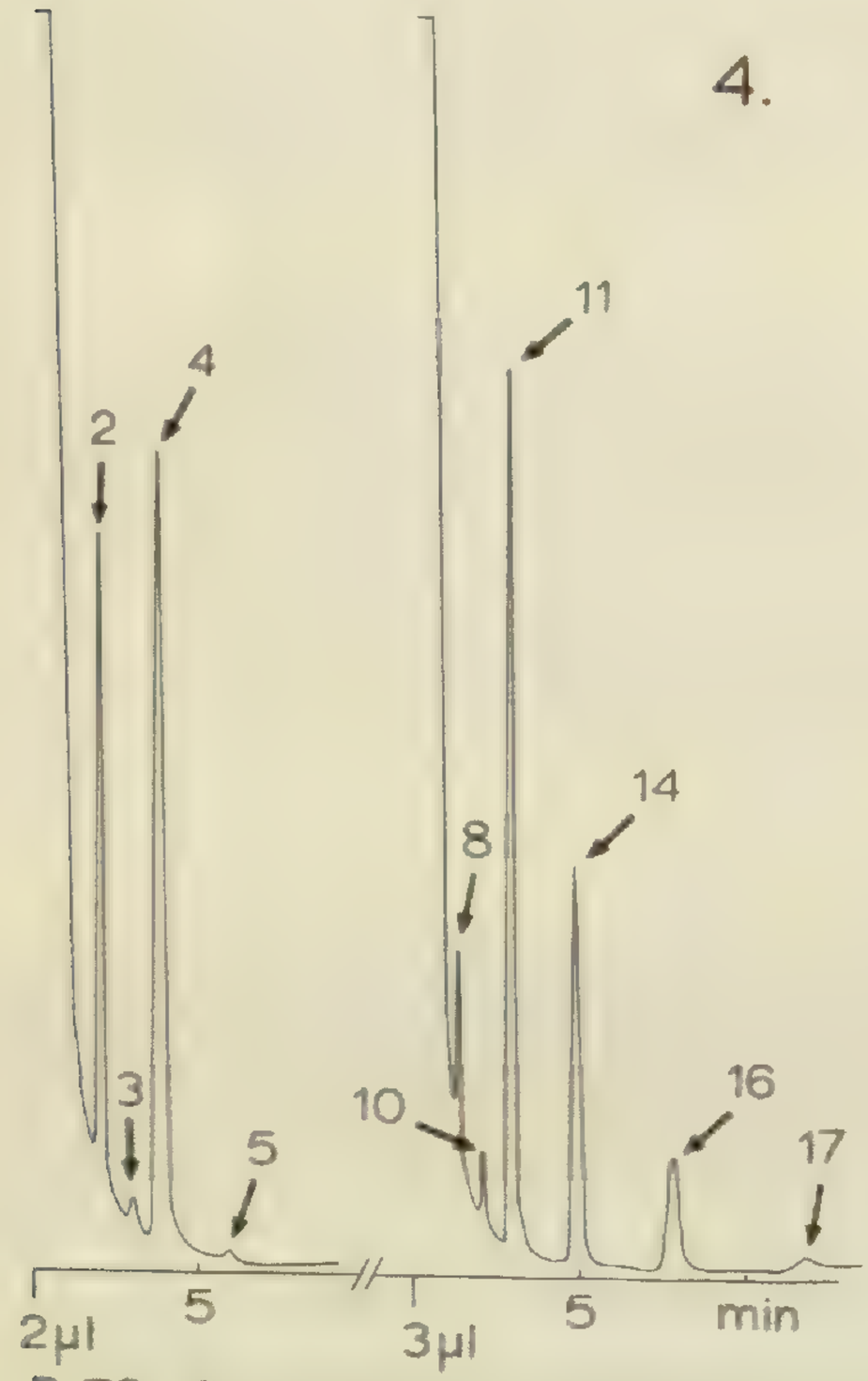


R-150: C. edentula ssp. edentula

2.

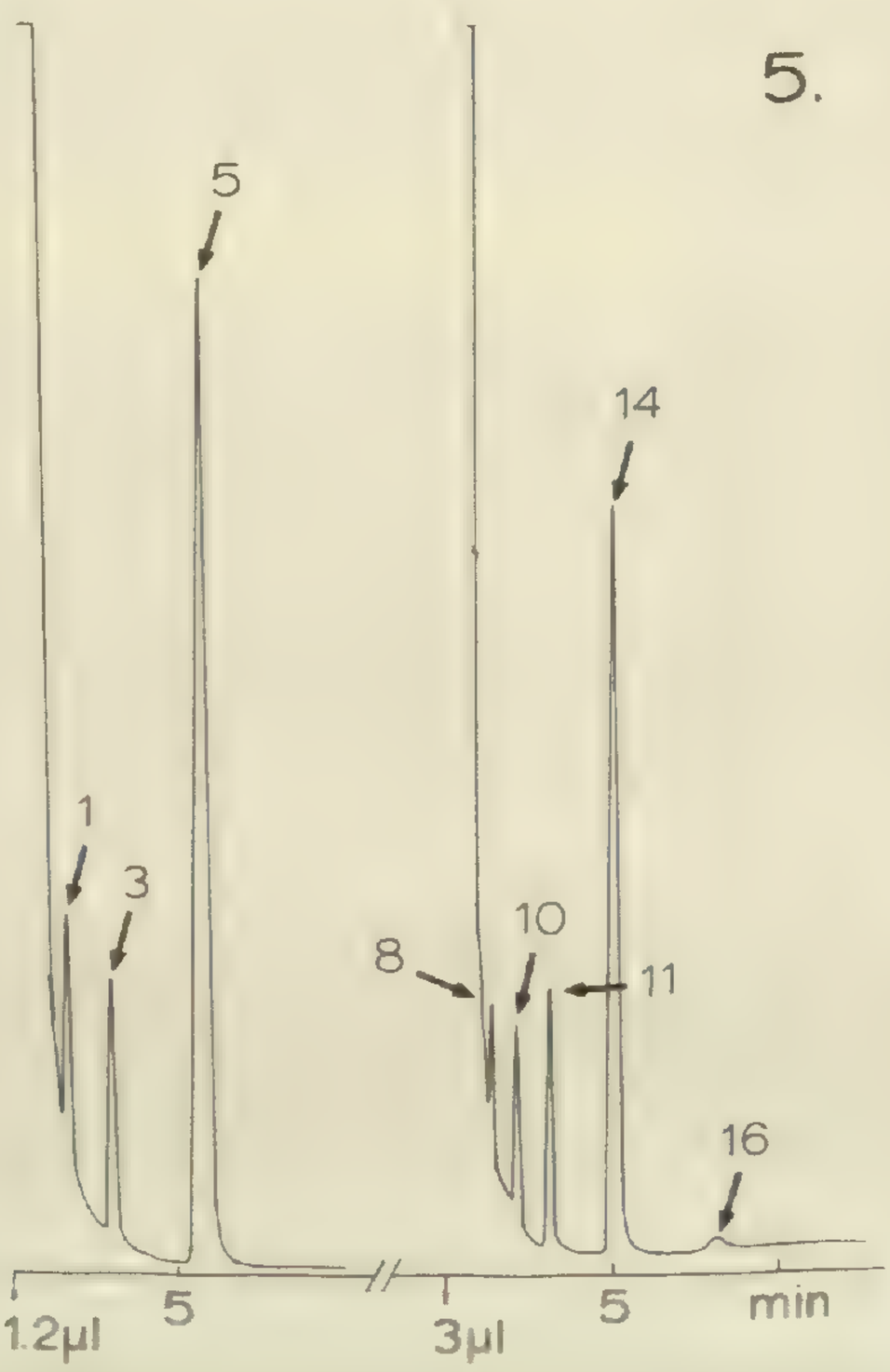
R-48: C edentula ssp. Harperi

3.



R-79: C. maritima ssp. maritima

4.



R-112: C. lanceolata ssp. lanceolata

5.

FIGS. 2–5. Gas chromatogram tracings of *Cakile* seed samples. 2. *C. edentula* ssp. *edentula;* 3. *C. edentula* ssp. *Harperi;* 4. *C. maritima* ssp. *maritima;* 5. *C. lanceolata* ssp. *lanceolata* (compounds as numbered in Table 15).

Cakile seeds does not, therefore, involve their array of glucosinolates. Thus, in the assessment of taxonomic similarities between plants, samples can be compared whether upper or lower seeds or a mixture of the two are analyzed.

In Tables 15 and 16 analyses done on mass samples are indicated by the collection number appearing in bold face. For these, seeds from 25 to 60 plants were used; in the remaining samples, one to ten plants contributed seeds for analysis. Single plants analyzed were samples 95/U, 95/L, 65a/L, 65b/L, 96/L, and 39/L in Table 15 and samples 87, 132, 133, 136/L, 95/L, 151/L, 150/L, 100/L, 39/U, 45/U, 45/L, 130/L, 62"P_1", 62"H", 62"P_2", 63a, 65a, 65b/L, 66/U, 66/L, F–41920/U, 114, 118, 127, and 128 in Table 16. No extensive analysis of intra-populational variation was made; for a few collections, however, one or two single plants were analyzed in addition to a mass sample, and for collection 62, believed to be a hybrid population of *C. geniculata* and *C. constricta*, a mass sample was investigated along with three individual plants suspected to be parental types and a hybrid intermediate. In these cases, the single-plant and mass samples possessed a similar array of glucosinolates although trace compounds were occasionally missed in one or the other. For example, in collection 95 (Table 15, *C. edentula* from Cape Cod) the single plant apparently lacked isopropylglucosinolate which appeared as a faint trace in the mass sample (the same quantity of seeds was used in both analyses). Similarly, in collection 96 (Table 15, *C. edentula* from Maryland) the single plant gave only faint evidence for the presence of 3-methylthiopropylglucosinolate which was conspicuous in the mass sample. The reverse situation, in which trace compounds were detected in a single plant but not in a mass sample, was also encountered. From Table 16, for example, sample 87, a single plant of West Coast *C. maritima*, shows 1.5% of Unknown 5, a compound not detected in other collections of this species from the Pacific Coast. Similarly, within the Jamaican collections of *C. lanceolata*, single plants 114 and 118 contained traces of Unknown 3 which was not found in other samples from the island. Examination of the results for the other single-plant analyses reveals that these possess a seed glucosinolate composition qualitatively and quantitatively similar to that of mass samples of that collection or of other collections of that taxon. For most of the North American sea rockets, interpopulational comparisons are based on analyses of mass samples. When they are not available, however, few-plant and single-plant samples can provide useful data for comparison, particularly when the samples are drawn from throughout the range of the taxa.

Comparing wild plants and plants grown in the greenhouse or growth chamber, the data indicate that the artificial conditions of cultivation do not affect the glucosinolate composition of the seeds. The qualitative array of compounds remains the same, and only minor quantitative variation appears. This is evident from Table 16 with collections 26

and 26–2 (*Cakile edentula* from Cape Cod) in which seeds from ten plants were analyzed for each sample (the "–2" indicates second-generation, greenhouse-grown plants), with collections 96 and 96–2 (*C. edentula* from Maryland) in which a wild mass sample and ten cultivated plants are compared, with collections 131 and 131–2 (*C. edentula* ssp. *Harperi* from Florida) in which a few plants were analyzed in each sample, and with collections W–9138 and W–9138–2 (*C. lanceolata* ssp. *fusiformis* from the Florida Keys) in which a few plants also were utilized for each analysis. These comparisons suggest that the glucosinolates are stable seed constituents under close genetic control and not easily modified environmentally. In the cultivated samples just cited as well as the rest in Table 16 identified by a "–2" after the collection number, the seeds were harvested from self-fertilized plants. This inbreeding apparently has no effect on the glucosinolate composition. Valid taxonomic comparisons can, therefore, be made between wild plant samples and samples of cultivated plants of *Cakile*. The conditions of cultivation may affect the total amount of glucosinolates present (cf. Kondra as cited in Josefsson 1971a), but the array of compounds and their relative concentrations appear to remain unchanged under the growing conditions I have employed.

In four of the samples, seeds were harvested from plants after two growth cycles, again involving self-fertilization, and these third-generation seeds were analyzed by gas chromatography. In Table 16 these are collections 24–3 (*Cakile edentula* ssp. *Harperi* from Florida), 25–3 (*C. geniculata* from Texas), R–s.n.–3 (*C. lanceolata* ssp. *lanceolata* from the Virgin Islands), and 29–3 (*C. maritima* ssp. *baltica* from Norway). The results are qualitatively similar to those of other collections of the corresponding taxon (the somewhat special case of collection 29–3 will be considered in more detail later). Whether the quantitative ratios are unrepresentative because of originally small sample sizes or inbreeding or both, or whether they are indeed accurate reflections of the glucosinolate composition of the populations from which these plants were derived could not be determined. The quantitative aspects of these analyses must, therefore, be treated cautiously.

To evaluate the taxonomic significance of seed glucosinolates in *Cakile*, the contents of Tables 15 and 16 must be integrated and interpreted. Toward that goal, Tables 17 and 18 were constructed by averaging the percentage composition of each glucosinolate encountered in the several analyses for each of the taxa investigated. In addition, Table 16 is divided into blocks representing geographic areas, and within an area the collections have been arranged in a directional order, usually by latitude, north to south. Seeds of *C. arabica* and *C. maritima* ssp. *euxina* were unfortunately not available for analysis; otherwise, all the taxa of *Cakile* have been investigated.

The first block in Table 16 presents the results of the sole Australian

sample analyzed, a collection from Black Rock, Victoria, made by Dr. Robert Parsons of LaTrobe University. Qualitatively and quantitatively, the pattern of seed glucosinolates is very similar to that of *Cakile maritima* ssp. *maritima* from the Pacific Coast of North America (Table 17), including the array of 3-, 4-, and 5-methylthioalkyl glucosinolates. Australian herbarium material of *C. maritima* is somewhat more variable morphologically than North American material; therefore, it would be interesting to have more glucosinolate data from Australian populations to check the variation in seed composition. The data available show that the naturalized *C. maritima*, in Australia and on the Pacific Coast of North America, has retained a full and similar complement of seed glucosinolates during its far-reaching migrations.

The second block in Table 16 comprises analyses of 12 collections from the Pacific Coast of North America, ranging from Oyster Bay, British Columbia (collection 28–2), to Ensenada, Baja California (collection 69). In addition, Table 15 presents the paper-chromatographic results from three West Coast samples (collections 94a and 94b from the same population in Oregon and a sample of *Cakile maritima* from California). The results fall into two distinct categories corresponding nicely to the morphologically recognized taxa, *C. maritima* ssp. *maritima* and *C. edentula* ssp. *edentula* var. *edentula*. *Cakile maritima* ssp. *maritima* contains principally *sec*-butylglucosinolate along with considerable amounts of isopropyl and 3-methylthiopropyl glucosinolates and conspicuous amounts of 4-methylthiobutyl and 5-methylthiopentyl glucosinolates. The next higher homologue in the ω-methylthioalkyl series, the 6-methylthiohexyl compound, constituted 1.4% of the isothiocyanate content of the single-plant sample of collection 87 and was also detected in trace amounts in three mass samples. Compounds of the ω-methylsulfinylalkyl series were also detected in *C. maritima* by paper chromatography. The homologous series of ω-methylthio- and ω-methylsulfinylalkyl glucosinolates constitute a distinctive feature of West Coast *C. maritima* ssp. *maritima* (and probably of Australian *C. maritima* as well). In addition, trace amounts of allyl isothiocyanate and of Unknowns 3 and 5 were regularly detected in Pacific Coast *C. maritima*, and traces of 3-butenyl isothiocyanate, constituting 4.4% of the Australian sample, were found in three mass samples. Since collection 87, a single plant sample, revealed six different known isothiocyanates by gas chromatography and since this method misses the ω-methylsulfinylalkyl glucosinolates which were found by paper chromatography of *C. maritima* samples, it is evident that individual plants of *C. maritima* ssp. *maritima* may possess up to nine different glucosinolates in their seeds. Such diversity in glucosinolate composition has not been reported previously.

The pattern of glucosinolate composition in naturalized *Cakile maritima* ssp. *maritima*, and in the one European sample of this subspecies which was available for analysis, is not the same as that of European *C. maritima*

TABLE 17. SEED GLUCOSINOLATE COMPOSITION OF THE TAXA OF CAKILE (AVERAGE PEAK-AREA PERCENTAGE BY GAS CHROMATOGRAPHY*) I.

Compound	C. maritima ssp. maritima (Australia; 1+0**)	C. maritima ssp. maritima (Pacific Coast; 7+2)	C. maritima ssp. maritima (North Sea; 1+0)	C. maritima ssp. baltica (3+0)	C. edentula var. edentula (Pacific Coast; 4+1)	C. edentula var. edentula (Atlantic Coast; 21+13)	C. edentula var. lacustris (3+0)	C. edentula ssp. Harperi (10+3)
1	0	0	0	0	0	0	0	7.9
2	18.3	18.5	T	T	T	1.9	T	0
3	5.5	T	8.9	85.7	70.9	80.2	93.9	3.2
4	60.5	50.4	91.1	12.5	26.5	16.7	4.4	T
5	4.4	T	0	T	1.0	1.1	1.0	84.7
6	0	0	0	T	T	1.2	T	0
7	0	0	0	0	0	0	0	1.6
8	0	T	0	0	0	0	0	T
9	0	0	0	0	T	T	T	T
10	T	T	0	0	0	0	0	T
11	1.5	15.8	0	T	1.6	1.6	T	T
12	0	0	0	0	0	0	0	T
13	0	0	0	0	T	T	T	0
14	7.9	9.3	0	0	0	0	0	1.5
15	0	0	0	0	0	0	0	T
16	2.0	5.3	0	0	0	0	0	T
17	0	T	0	0	0	0	0	0
18	N.D.	P	N.D.	N.D.	0	0	N.D.	0
19	N.D.	P	N.D.	N.D.	0	0	N.D.	P
20	N.D.	P	N.D.	N.D.	0	0	N.D.	0
21	N.D.	0	N.D.	N.D.	0	0	N.D.	?

Legend: *excluding compounds 18–21, determined by paper chromatography; ** number of gas-chromatographic samples + number of paper chromatographic samples; T trace amounts present; N.D. not determined; P present.

ssp. *baltica* (Table 17). Published information on glucosinolates of *C. maritima* does not, unfortunately, provide much data for confirming this difference. Of the five reports on glucosinolates in this species, three are not comparable with the seed analyses discussed here. Wright (1927), who probably studied British plants, reported ". . . the characteristic odour of Allyl isothiocyanate . . ." from enzymatic hydrolysates of vegetative and floral tissues. Delaveau (1957), who analyzed immature whole fruits from plants in a Paris botanical garden by the method of paper chromatography in one solvent system, detected seven different compounds, four of which he tentatively identified as allyl, 3-butenyl, 4-pentenyl, and 2-phenylethyl isothiocyanates. And Schraudolf (1968), also analyzing material of unreported provenance, found three indole

glucosinolates in etiolated seedlings. The remaining two reports concern seed composition. Kjær, Conti, and Larsen (1953), analyzing seeds of plants from the University of Copenhagen Botanical Garden, detected allyl isothiocyanate as the sole product of enzymatic hydrolysis. Danielak and Borkowski (1969) also reported allylglucosinolate as the sole constituent, from plants of unidentified (and unknown?) provenance. The last block of Table 16 shows the results of my analyses of three samples of European *C. maritima* ssp. *baltica* (collections 29–3, 153, and 154) and of one sample of *C. maritima* ssp. *maritima* (collection 152 from the North Sea coast of Denmark, a sample of less than 0.2 g of partly fungus-infected seed). Sample 29–3, from greenhouse plants, originated from seeds of a few plants collected in southeastern Norway, and samples 153 and 154 comprised seeds of a few plants collected from close populations on the Kattegat coast of Denmark (cf. Appendix I). The composition, with allylglucosinolate the principal compound, is clearly distinct from *C. maritima* ssp. *maritima* of western Denmark, the Pacific Coast, and Australia. Indeed, the pattern is very similar to that found in *C. edentula* ssp. *edentula* (to be discussed later). Unfortunately, no results have been reported from plants of the Mediterranean Coast. The Mediterranean littoral is the most likely source area of the introduced *C. maritima* on the Pacific Coast of North America and in Australia. The available data from northern European and naturalized populations of *C. maritima* establish the existence of chemical races in this species, corresponding to the morphologically recognized subspecies, *maritima* and *baltica*. Geographical variation in the cultivated species *Brassica juncea* was reported by Hemingway, Schofield, and Vaughan (1961) after an extensive paper-chromatographic investigation of two seed glucosinolates, and recently Kjær, Schuster, and Park (1971) proposed that the introduced *Lepidium bonariense* in Queensland, Australia, constitutes a chemical race of this native of South America. Additional analyses on populations of Old World *Cakile maritima* (especially the Black Sea *C. maritima* ssp. *euxina*) will be needed to fully substantiate the pattern of differentiation revealed here. Such an investigation may help to pinpoint the source area of the naturalized *C. maritima* on the Pacific Coast of North America and in Australia. At the present time, the chemical results support the recognition of infraspecific taxa in this species.

The other introduced sea rocket on the Pacific Coast of North America, *Cakile edentula* ssp. *edentula* var. *edentula*, is represented by samples 28–2/U, 91, 89, and 94a/U in Table 16 and by sample 94a/L in Table 15. The samples are qualitatively nearly identical (possessing isopropyl, allyl, *sec*-butyl, 3-butenyl, 3-methylthiopropyl, and benzyl glucosinolates) and are quantitatively similar except for the ratios of allyl and *sec*-butyl glucosinolates, the two major constituents. The composition is quite distinct from that of *C. maritima* ssp. *maritima* (Table 17), and in mixed populations the two taxa maintain their chemical identity, as samples

94a and 94b from Oregon demonstrate (Table 15). The two major glucosinolates in seeds of Pacific Coast *C. edentula* var. *edentula* vary inversely in proportion and clinally over the range of the four populations sampled (cf. the second block in Table 16 where the samples are listed from north to south). The situation parallels that for *C. edentula* var. *edentula* on the Atlantic Coast where northern populations usually exhibit more *sec*-butylglucosinolate and less allylglucosinolate than southern populations. On the Atlantic Coast, however, the change does not appear to be clinal but abrupt instead, occurring in the region of Cape Cod. Clinal variation in glucosinolate content has not been reported previously, and its functional significance (if any) is unknown. If the four samples analyzed are truly representative of West Coast *C. edentula*, the results strongly suggest that natural selection for glucosinolate composition, operating through the agency of some environmental factor(s) correlated with latitude, has created the clinal pattern observed in these naturalized populations.

The glucosinolate composition of Pacific Coast *Cakile edentula* is qualitatively similar to that of Great Lakes populations of *C. edentula* ssp. *edentula* var. *lacustris* and that of typical *C. edentula* on the Atlantic Coast of North America (Table 17). The Great Lakes sea rockets are represented by single-plant samples 132 and 133 and the greenhouse collection 102–2/U in the third block of Table 16; sample 27–2, originating from Baie St. Paul on the St. Lawrence River, appears on morphological grounds to be *C. edentula* var. *lacustris* and is included here. The samples are quite uniform, with allylglucosinolate the principal constituent along with much smaller amounts of *sec*-butylglucosinolate and small or trace amounts of isopropyl, 3-butenyl, 3-methylthiopropyl, and benzyl glucosinolates and Unknown 4. The trace occurrence of 4-methylthiobutyl isothiocyanate in sample 102–2 and 5-methylthiopentyl isothiocyanate in single-plant sample 133—compounds which were not detected in any other samples of *C. edentula* ssp. *edentula*—should alert one to the caution that must be used in asserting that the absence of a particular compound is characteristic of a taxon. First, the absence of any compound is always relative to the sensitivity of the analytical method employed. Second, the sporadic occurrence of some compounds may represent nothing more than "noise" in the biosynthetic machinery of the organism, understandable if more were known of the precursors, metabolic pathways, and enzymatic specificities involved. In this instance, the two compounds are not anomalous since the lower homologue, 3-methylthiopropylglucosinolate, occurs regularly in seeds of *C. edentula.*

The fourth block of Table 16 presents the results of collections, listed from north to south, from the Atlantic Coast of North America, with samples 31–2 from Nova Scotia to 39 from North Carolina constituting *Cakile edentula* ssp. *edentula* var. *edentula* (Table 17). Nine of these 16 populations were also analyzed by paper chromatography with the

results shown in Table 15. The samples are qualitatively homogeneous, but the quantitative ratios of four glucosinolates indicate geographical variation within this taxon. Five of the six northernmost collections (the single-plant sample 136/L being exceptional) contain 40-55% allylglucosinolate and 40–60% *sec*-butylglucosinolate; in addition, they possess slightly more isopropylglucosinolate and lack Unknown 2. The transition to this pattern of glucosinolate content occurs rather abruptly in Massachusetts, from population 95 on Cape Cod Bay to population 104 at Nahant, north of Boston. Cape Cod has long been recognized as a natural boundary for many organisms (Burk 1968), and the change in glucosinolate composition within *C. edentula* var. *edentula* in this area may be a response to some environmental factor correlated with this geological feature. Alternatively, the change may have no ecological significance but constitute instead a founders' effect, arising from the northward migration of chemically variant elements of *C. edentula* following the retreat of the Pleistocene glaciers. Whatever the cause, the change is expressed on the population level since individual plants, as sample 136 demonstrates, may be similar to southern collections. No morphological characters correlated with this pattern of glucosinolate composition have been discerned.

The only other published account of glucosinolates in the genus *Cakile*, in addition to the ones for *C. maritima* cited previously, is a report by Daxenbichler *et al.* (1964) on a sample of *C. edentula* collected in Virginia (Dr. Arthur Barclay, personal communication; most certainly, therefore, *C. edentula* ssp. *edentula* var. *edentula*). Using a method of paper chromatography essentially identical to the one I have employed but with only a single solvent system, water-saturated chloroform, they detected three compounds derived from seeds: an unidentified constituent remaining at the point of extract application (possibly 3-methylsulfinylpropylthiourea, which I tentatively identified in sample 39 from North Carolina; Table 15); allylthiourea, the predominant compound; and *sec*-butylthiourea, a trace constituent. The latter compound, with an R_{Ph} of 0.74 ± 0.03, cannot be distinguished in chloroform, however, from 3-methylthiopropylthiourea, which has an R_{Ph} of 0.75. In either case, the results are in perfect accord with those for *C. edentula* ssp. *edentula* var. *edentula* presented here. Daxenbichler *et al.* also measured the absolute amount of glucosinolates present in the seeds and reported 21.6 mg of volatile isothiocyanates per gram of defatted seed meal in *C. edentula*, which was the highest value obtained from the 65 species of Cruciferae investigated.

In collections from the Outer Banks of North Carolina (39, 40, and 41 in Table 16) there occurs a conspicuous change in glucosinolate composition marked by the increasing predominance of 3-butenylglucosinolate and the corresponding decrease in allyl and *sec*-butyl glucosinolates. The new pattern of glucosinolate composition continues southward through

all the populations of *Cakile edentula* ssp. *Harperi* sampled (collections 40 to 48, arranged from north to south, in the fourth block of Table 16). Five of the nine populations sampled were also analyzed by paper chromatography (Table 15). The predominant compound in seeds of *C. edentula* ssp. *Harperi* is 3-butenylglucosinolate; allylglucosinolate constitutes less than 5% of the total seed composition. Unknown 1 is a conspicuous compound; it was found in nearly all samples of the genus in which 3-butenylglucosinolate occurred in significant amounts. The homologous series of 3-, 4-, and 5-methylthioalkyl glucosinolates and the corresponding 4-methylsulfinylbutylglucosinolate (judging from the paper-chromatographic results) are characteristic for this subspecies, and the related 4-methylsulfonylbutylglucosinolate may also occur regularly in trace amounts. Small amounts of 4-pentenylglucosinolate along with traces of

TABLE 18. SEED GLUCOSINOLATE COMPOSITION OF THE TAXA OF CAKILE (AVERAGE PEAK-AREA PERCENTAGE BY GAS CHROMATOGRAPHY*) II.

Compound	C. arctica (Iceland; 1+0)**	C. constricta (4+1)	C. geniculata (6+2)	C. lanceolata ssp. lanceolata (11+2)	C. lanceolata ssp. fusiformis (9+2)	C. lanceolata ssp. pseudoconstricta (2+1)	C. lanceolata ssp. alacranensis (1+0)	C. lanceolata (Bermuda; 2+0)
1	0	5.1	5.3	5.9	6.0	7.9	0	1.7
2	0	0	0	0	0	0	0	0
3	92.2	9.4	20.2	7.4	8.5	5.1	0	62.4
4	0	5.8	T	T	T	T	0	34.6
5	T	75.5	70.5	78.8	78.2	82.0	52.7	T
6	T	0	0	0	0	0	0	0
7	0	0	0	T	T	T	0	0
8	T	T	T	T	T	T	0	0
9	T	0	T	T	0	0	0	0
10	T	3.5	T	T	2.0	1.7	T	0
11	6.4	T	1.8	1.6	1.3	T	0	T
12	0	T	0	T	T	T	0	0
13	0	0	0	0	0	0	0	0
14	T	2.7	1.7	6.1	4.0	1.5	47.3	T
15	T	0	0	T	0	0	0	0
16	0	T	0	T	T	T	0	0
17	0	0	0	0	0	0	0	0
18	N.D.	0	0	0	0	0	N.D.	N.D.
19	N.D.	?	0	0	0	0	N.D.	N.D.
20	N.D.	0	0	0	0	0	N.D.	N.D.
21	N.D.	0	0	0	0	0	N.D.	N.D.

Legend: *excluding compounds 18–21, determined by paper chromatography; ** number of gas-chromatographic samples + number of paper-chromatographic samples; T trace amounts present; N.D. not determined.

2-phenylethylglucosinolate are also characteristic, occurring only sporadically as traces in a few other taxa. The results from sample 45 (Table 15 and 16) indicate that individual plants of *C. edentula* ssp. *Harperi* may possess at least 10 different known glucosinolates in their seeds. The chemical composition is summarized in Table 17, and a typical gas-chromatogram is presented in Figure 3.

Mixed populations of *Cakile edentula* ssp. *edentula* and *C. edentula* ssp. *Harperi* were found in Dare County (collection 40) and Hyde County (collection 41) in northern North Carolina, and the results of the glucosinolate analyses (Table 16) show a nice transition between the two taxa, particularly in the amounts of allyl and 3-butenyl glucosinolates, in these populations. It is not evident whether the intermediate results are due to varying proportions of the two subspecies or to hybridization. No chemical analysis of individual wild plants was undertaken although field observations on fruit length did suggest the presence of hybrids. Artificial hybrids of the two taxa have been produced (see section on hybridization), and an analysis of seed glucosinolates of two F_1 plants gave the nicely intermediate results presented in Table 19. Glucosinolate analysis would thus appear to be a useful tool in the study of hybrid populations.

The glucosinolate composition of populations south of *Cakile edentula* ssp. *Harperi* on the Atlantic Coast of Florida (collections 49 to 53, Table 16) does not differ as dramatically from that of this taxon as does *C. edentula* ssp. *edentula* north of it. Indeed, throughout the region of the Gulf of Mexico (block five in Table 16) and the West Indies (blocks six through ten) the same qualitative array of glucosinolates is encountered, and only slight quantitative differences distinguish the taxa. The chemical data will seem disappointing to the taxonomist seeking constant characters facilitating the recognition of natural units. The systematist, however, acknowledges that all characters are subject to variation and that natural units must be defined polythetically, without reliance on any one set of attributes.

Samples 49 and 50 from Brevard and Indian River Counties, Florida, and samples 58 and 60 from western Florida represent the new species, *Cakile constricta*. Small amounts of *sec*-butylglucosinolate distinguish three of the four samples; collection 58 apparently lacks this compound. The pattern of seed glucosinolates is similar to that of *C. lanceolata* in Florida and the West Indies, to which the new species is probably phyletically related.

The fifth block in Table 16 lists collections from the shores of the Gulf of Mexico, proceeding from population 56 in southwestern Florida (Lee County) counterclockwise around the Gulf to sample F–41920 from the Alacrans off the coast of Yucatan. The latter, representing *Cakile lanceolata* ssp. *alacranensis*, comprised a small sample of seeds taken from a 12-year old herbarium specimen (*Fosberg 41920*, US). Three

compounds were detected: 3-butenylglucosinolate, the predominant one; Unknown 5 in trace amounts; and a large amount of 4-methylthiobutylglucosinolate. Qualitatively, the array is typical of other collections of *C. lanceolata*; the conspicuous quantity of 4-methylthiobutylglucosinolate may be characteristic, however, for this subspecies. While herbarium materials, even old ones, can often be relied on to give an accurate sample of the major seed glucosinolates present in a taxon (Dr. Ihsan Al-Shehbaz, unpublished results), more analyses, particularly of recent collections, are needed to establish the chemical identity of *C. lanceolata* ssp. *alacranensis*.

Cakile geniculata, ranging along the Gulf strand from Louisiana and Texas south to Veracruz, is represented in Tables 15 and 16 only by single-plant or few-plant samples. Field work in Louisiana and Texas during the summer of 1969 resulted in consistently finding this species in mixed populations with *C. constricta* or with *C. lanceolata* ssp. *psuedoconstricta*. Moreover, plants with intermediate morphological features were readily found, suggesting extensive hybridization (see section on hybridization). The glucosinolate composition of pure *C. geniculata*, therefore, may never be known with certainty. In Table 16 collections of what appeared to be distinct *C. geniculata* include 63a (a single plant from Cameron Parish, Louisiana), 25–3 (ca. ten growth-chamber plants grown from seed originally collected from Galveston, Texas), 65a and 66 (single plants from Mustang Island, Texas), and 129–2 (ca. ten growth-chamber plants grown from seed originally collected from a single plant in Veracruz). In addition, Table 15 presents the paper-chromatographic results (Ettlinger & Thompson, personal communication) from an analysis of a sample from Tamaulipas. The qualitative composition of glucosinolates is similar to that of *C. lanceolata* (Table 18) except in the lack of traces of 4-pentenyl, Unknown 6, and 5-methylthiopentyl glucosinolates. Quantitatively, *C. geniculata* possesses distinctively high amounts of allylglucosinolate. Only sample 66 deviates from this pattern. Morphologically, fruits of this collection varied in size and shape toward *C. lanceolata* ssp. *pseudoconstricta*, and the plant may have been of hybrid origin.

Eleven collections in Table 16 represent *Cakile lanceolata* ssp. *lanceolata* from the West Indies. Qualitatively and quantitatively, the glucosinolate composition is consistent throughout this area and nearly identical to that of *C. lanceolata* ssp. *fusiformis* in southern Florida and of *C. lanceolata* ssp. *pseudoconstricta* on the Gulf strand. Table 18 summarizes the pattern of seed glucosinolate composition in these taxa, and a typical gas chromatogram is presented in Figure 5. Some geographical differentiation is indicated by the results from the Bahamian collections; these samples (32, 33, and B–103) contained minor amounts of 2-phenylethylglucosinolate, which was not encountered in any other samples of *C. lanceolata*.

The two single-plant samples of *Cakile lanceolata* from Bermuda (collections 127 and 128 in Table 16) gave chemically anomalous results. The pattern is unique, with allylglucosinolate the predominant compound, large amounts of *sec*-butyl and small amounts of Unknown 1, 3-methylthiopropyl, and 4-methylthiobutyl glucosinolates, and only traces of 3-butenylglucosinolate. The plants were morphologically peculiar, having short fruits and nearly entire, very succulent leaves. Pobedimova (1963, 1964) remarked on the heterogeneity of herbarium collections from Bermuda, and I am also unable to place all the specimens in one or even two of the subspecies of *C. lanceolata*. It would appear that local differentiation in both chemical and morphological characters has occurred in Bermuda populations but that repeated introductions of typical *C. lanceolata* ssp. *lanceolata* and *C. lanceolata* ssp. *fusiformis* (via the Gulf Stream?) have suppressed tendencies toward the evolution of a distinct Bermuda race.

A single sample of *Cakile arctica* was analyzed from growth-chamber plants originating from seed collected in Iceland, with results presented in Table 16. The glucosinolate composition is distinctive. However, it would be imprudent to assume this single sample is characteristic of *C. arctica* as a whole. Morphologically, the species is distinct and in particular does not greatly resemble *C. edentula*. The chemical data, meager as they are, support a separation of the two species, which I am maintaining on morphological and phenological evidence.

The biogenesis of only a few glucosinolates is known in any detail, but what work has been done corroborates the hypothesis that these natural products are derived from α-amino acids or their homologues with side chains corresponding to the "R" of the generalized glucosinolate structure (Ettlinger & Kjær 1968). A variation prevails with the alkenyl glucosinolates (e.g., allyl, 3-butenyl, and 4-pentenyl glucosinolates) which probably arise from homologues of methionine by loss of the ω-methylthio group and concurrent formation of the double bond (Chisholm & Matsuo 1972; Josefsson 1971b). Consequently, the seed glucosinolates of *Cakile* most likely originate biosynthetically from the amino acids valine, isoleucine, homomethionine and its higher homologues, phenylalanine, and 2-amino-4-phenylbutyric acid. In only a few instances does a particular biosynthetic pathway characterize a taxon; in general, the array of glucosinolates is similar throughout the genus, and it is quantitative shifts in the production of certain compounds which have created the distinctive patterns of glucosinolate composition. An example of a unique biosynthetic pathway occurs in *C. edentula* ssp. *edentula* where benzylglucosinolate, derived most likely from phenylalanine (Underhill, Chisholm & Wetter 1962), was detected. Interestingly, phenylethylglucosinolate, which may be biosynthetically related to benzylglucosinolate, is characteristic of *C. edentula* ssp. *Harperi*. For the major glucosinolates of the genus (e.g., allyl, *sec*-butyl, and 3-butenyl

TABLE 19. SEED ISOTHIOCYANATE COMPOSITION OF ARTIFICIAL F_1 HYBRIDS OF CAKILE EDENTULA SSP. EDENTULA AND C. EDENTULA SSP. HARPERI (PEAK-AREA PERCENTAGE BY GAS CHROMATOGRAPHY.)

Compound R	C. edentula ssp. edentula (34-2/U)	F_1-L1	F_1-L4	C. edentula ssp. Harperi (24-3)
Unknown 1	0	2.7	1.5	13.4
$(CH_3)_2CH$	1.0	0.4	0.4	0
$CH_2{=}CHCH_2$	45.6	12.6	13.5	4.4
$C_2H_5CH(CH_3)$	53.1	34.6	32.9	0.3
$CH_2{=}CH(CH_2)_2$	T	49.7	51.7	78.9
Unknown 2	0	0	0	0
$CH_2{=}CH(CH_2)_3$	0	0	0	1.3
Unknown 3	0	0	0	T
Unknown 4	0	0	0	0
Unknown 5	0	0	0	0
$CH_3S(CH_2)_2$	T	T	T	0.6
Unknown 6	0	0	0	T
$C_6H_5CH_2$	0	0	0	0
$CH_3S(CH_2)_4$	0	T	T	T
$C_6H_5(CH_2)_2$	0	T	T	T
$CH_3S(CH_2)_5$	0	0	0	T
$CH_3S(CH_2)_6$	0	0	0	0

T = trace amounts present.

TABLE 20. SEED ISOTHIOCYANATE COMPOSITION OF AN ARTIFICIAL F_1 HYBRID OF CAKILE EDENTULA SSP. EDENTULA AND C. LANCEOLATA SSP. LANCEOLATA (PEAK-AREA PERCENTAGE BY GAS CHROMATOGRAPHY.)

Compound R	C. edentula ssp. edentula (26-2)	F_1	C. lanceolata ssp. lanceolata (R-s.n.-3)
Unknown 1	0	3.7	2.6
$(CH_3)_2CH$	T	T	0
$CH_2{=}CHCH_2$	89.8	36.0	0.8
$C_2H_5CH(CH_3)$	6.0	3.2	0
$CH_2{=}CH(CH_2)_2$	0.8	56.6	95.0
Unknown 2	0.4	0	0
$CH_2{=}CH(CH_2)_3$	0	0	T
Unknown 3	0	T	T
Unknown 4	T	0	0
Unknown 5	0	0	T
$CH_3S(CH_2)_3$	2.8	T	T
Unknown 6	0	0	T
$C_6H_5CH_2$	T	T	0
$CH_3S(CH_2)_4$	0	T	1.4
$C_6H_5(CH_2)_2$	0	0	0
$CH_3S(CH_2)_5$	0	0	T
$CH_3S(CH_2)_6$	0	0	0

T = trace amounts present.

TABLE 21. SEED ISOTHIOCYANATE COMPOSITION OF ARTIFICIAL F_1 HYBRIDS OF CAKILE EDENTULA SSP. EDENTULA AND C. LANCEOLATA SSP. FUSIFORMIS (PEAK-AREA PERCENTAGE BY GAS CHROMATOGRAPHY.)

Compound R	C. edentula ssp. edentula (26-2)	F_1-L7	F_1-U14	C. lanceolata ssp. fusiformis (W-9138-2)
Unknown 1	0	3.0	5.2	8.6
$(CH_3)_2CH$	T	0	0	0
$CH_2=CHCH_2$	89.8	54.6	32.9	9.2
$C_2H_5CH(CH_3)$	6.0	1.2	0.7	0
$CH_2=CH(CH_2)_2$	0.8	40.9	60.1	76.3
Unknown 2	0.4	0	0	0
$CH_2=CH(CH_2)_3$	0	0	0	0
Unknown 3	0	0	0	T
Unknown 4	T	0	T	0
Unknown 5	0	T	0	1.0
$CH_3S(CH_2)_3$	2.8	T	T	1.1
Unknown 6	0	0	0	T
$C_6H_5CH_2$	0.2	0	0	0
$CH_3S(CH_2)_4$	0	0	T	3.6
$C_6H_5(CH_2)_2$	0	0	0	0
$CH_3S(CH_2)_5$	0	0	0	T
$CH_3S(CH_2)_6$	0	0	0	0

T = trace amounts present.

glucosinolates) it is shifts in their relative concentrations, not presence vs. absence, which characterize the individual taxa.

The glucosinolate composition of interspecific hybrids has apparently been reported only for cultivated species of the genus *Brassica* (Kjær & Hansen 1958; Josefsson & Jönsson 1969). Tables 19, 20, and 21 present the results of my gas-chromatographic analyses of seeds from artificial F_1 hybrid plants produced from crosses between *Cakile edentula* ssp. *edentula* var. *edentula* and *C. edentula* ssp. *Harperi*, between *C. edentula* ssp. *edentula* and *C. lanceolata* ssp. *lanceolata*, and between *C. edentula* ssp. *edentula* and *C. lanceolata* ssp. *fusiformis*. The isothiocyanate composition of the parents was determined from seeds harvested from a few growth-chamber plants of the parental collections. The results demonstrate beautifully that F_1 hybrids possess a qualitatively additive array of glucosinolates with quantitative ratios intermediate between the parents. The chemically intermediate nature of samples 40 and 41 from the Outer Banks of North Carolina has already been described. Table 16 shows the gas-chromatographic results from an analysis of mass sample 62 (Grand Isle, Louisiana) and of three single-plant samples corresponding morphologically to *C. geniculata* (62 "P_2"), *C. constricta* (62 "P_1"), and a suspected hybrid (62 "H"). The mass sample was quantitatively intermediate between the averages for the two parental species (Table 18) for seven of the 11 volatile compounds detected in seeds of these taxa (allyl, *sec*-butyl, 3-butenyl, 3-methylthiopropyl, and 4-methyl-

thiobutyl isothiocyanates and Unknowns 5 and 6). The single-plant samples, however, were not clearly representative of the species to which they correspond morphologically, nor was the putative hybrid chemically intermediate. Such a heterogeneous pattern suggests introgression. The two species suspected of hybridizing here are not very distinct in glucosinolate composition; it is, therefore, difficult to distinguish between the effects of hybridization (and introgression) and normal quantitative variation. Where differences are greater, as in the populations from the Outer Banks, glucosinolate analysis should prove to be a useful tool in the study of natural hybridization.

In summary, this chromatographic investigation of seed glucosinolates in the genus *Cakile* shows the potential that analysis of these compounds offers for taxonomic studies. The glucosinolates were found to be stable under a variety of environmental conditions and consistently present in populations of a taxon. Single plants usually contain the full complement of compounds found in mass samples. No differences were detected between the dimorphic seeds of *Cakile*. For most of the taxa investigated (*C. arabica* and *C. maritima* ssp. *euxina* were not available for analysis) distinctive qualitative and/or quantitative patterns of composition were revealed. Interspecific differences are often dramatic, e.g., between *C. arctica* and *C. lanceolata*, which are morphologically distinct as well. Differences between other morphologically distinct taxa, as in the West Indian and Gulf of Mexico sea rockets, are not as great, and the seed compositions of *C. edentula* ssp. *edentula* and *C. maritima* ssp. *baltica* are virtually the same and may reflect their geologically recent phyletic divergence (see section on evolution). Intraspecific variation, correlated with morphologically recognized subspecies, was found in *C. edentula*, *C. maritima*, and *C. lanceolata*. Geographic variation in glucosinolate content without a morphological counterpart was detected in Atlantic Coast *C. edentula* ssp. *edentula* and in Pacific Coast *C. edentula* where it appears to be clinal. Preliminary studies of artificial and putative natural hybrids encourage the use of glucosinolate analysis as a tool in the study of natural hybridization. The investigations thus demonstrate that glucosinolate characters are similar to other kinds of characters in their patterns of distribution, susceptibility to variation, and usefulness as taxonomic markers.

Growth Cycle

All the species of *Cakile* grow as herbaceous annuals or, under exceptionally favorable circumstances, as "fortuitous perennials" (Radford, Ahles & Bell 1968). Barbour (1970d), for example, reported that a few plants of naturalized *C. maritima* in California survived the winter at Bodega Bay to flower again the following spring. While the plants have been described as annuals or biennials in some floristic works (Standley & Steyermark 1946; Leon & Alain 1951), the term biennial is inappropriately applied to sea rockets since it properly denotes a plant which

remains vegetative the first year, then flowers and dies the second. All the plants of *Cakile* which I have cultivated flowered and fruited within two months of germination. In nature, the plants undoubtedly grow from seed to fruit uninterrupted by a period of vegetative dormancy. Perhaps the sea rockets should best be described as facultative annuals.

At middle and northern latitudes the sea rockets usually germinate in the early spring, and the plants flower and fruit toward the end of summer and into autumn. Germination may depend, at least in part, on a critical amount of precipitation, as Barbour (1972) has suggested for *Cakile maritima*. At subtropical latitudes the growth cycle is less seasonally defined, and plants may be found in flower and fruit nearly throughout the year. Winter storms in the Gulf of Mexico, however, seem to impress a general regimen upon the Gulf sea rockets. Sauer (1967, 1972) speculated that the annual growth cycle of *Cakile*, an anomalous habit in the tropical strand vegetation, betrays its temperate origins but also preadapted the plants to the pattern of seasonal storms in the Gulf of Mexico. Few observations have been recorded of the inland species, *C. arabica*; it would be interesting to know the relationship between seed germination and rainfall in this desert species.

While differences in the length of the growth cycle between the taxa of *Cakile* may exist, this could not be investigated in the field. However, most of the taxa have been cultivated under uniform environmental conditions (usually in growth chambers), and the growth cycles under these artificial circumstances can be compared. The differences thus exposed, in addition to being taxonomically interesting, may have adaptive significance for the breeding systems of sea rockets. Over a period of four years (1968–1971) many collections were grown under various growth-chamber or greenhouse conditions. Twenty-six of these cultures were sufficiently uniform to permit comparison. In these cases seeds (six months to two years old) were sown ¼- to ½-inch deep in vermiculite or perlite in a Sherer Controlled Environment Chamber with a 16-hour photoperiod, transplanted as seedlings to sand or sand:perlite in 2-inch pots, and grown under a 16-hr photoperiod (incandescent and fluorescent lights, ca. 2400 foot-candles, with day temperatures at 25° C. and night temperatures at 21° C. and 70% relative humidity) with ¼ strength Hoagland's solution. The average number of days until flowering from date of sowing is presented in Table 22, with the taxa ranked from shortest period to longest. Table 23 records average maturation time (time to flowering) for all the growth-chamber cultures; for the additional 18 cultures, seeds were sown in the 8-hr or 12-hr growth chambers or in Petrie dishes at room temperature and the seedlings subsequently transplanted to sand-filled pots in growth chambers under 8-, 12-, or 16-hr photoperiods. No photoperiodic effect on flowering was observed in any of the taxa (Barbour 1970d). The results in Table 22 generally correspond to those of Table 23.

The differences demonstrated in Tables 22 and 23 are of limited

TABLE 22. AVERAGE TIME FROM SOWING TO FLOWERING OF THE TAXA OF CAKILE GROWN UNDER 16 HOURS OF LIGHT IN GROWTH CHAMBER.

Taxon	No. of cultures	No. of plants	No. of days	Range
C. arctica	2	11	21	20–22
C. maritima ssp. maritima (Pacific Coast)	3	23	32	28–35
C. maritima ssp. baltica	1	8	32	
C. edentula ssp. Harperi	1	6	33	
C. lanceolata ssp. lanceolata	6	42	36	31–42
C. lanceolata ssp. fusiformis	3	14	36	34–38
C. edentula ssp. edentula (Pacific Coast)	2	25	36	33–39
C. geniculata	1	6	38	
C. constricta	2	15	39	33–45
C. edentula var. lacustris	2	19	43	40–45
C. edentula var. edentula	3	29	44	40–49

TABLE 23. AVERAGE TIME FROM SOWING TO FLOWERING OF THE TAXA OF CAKILE GROWN UNDER 8, 12, OR 16 HOURS OF LIGHT IN GROWTH CHAMBER.

Taxon	No. of cultures	No. of plants	No. of days	Range
C. arctica	3	33	21	20–22
C. maritima ssp. maritima (Pacific Coast)	3	38	32	28–35
C. maritima ssp. baltica	2	39	35	32–38
C. lanceolata ssp. lanceolata	10	103	36	31–42
C. edentula ssp. edentula (Pacific Coast)	2	25	36	33–39
C. edentula ssp. Harperi	3	40	38	33–40
C. lanceolata ssp. fusiformis	7	68	38	34–45
C. constricta	2	15	39	33–45
C. edentula var. lacustris	2	33	43	40–45
C. edentula var. edentula	7	81	44	37–52
C. geniculata	3	20	44	38–49

taxonomic importance because of the small number of cultures, but certain results may be significant. Most notable was the very short maturation time in *Cakile arctica* (based on collections from Iceland); the 21-day average is only half that of the average time of *C. edentula* ssp. *edentula*, with which these northern plants are often confused. The short maturation time in *C. arctica* may reflect an adaptation to the restricted season of growth available to these plants of high northern latitudes. Since it might be expected that taxa of higher latitudes with more pronounced seasons would adapt with shorter growth cycles, it appears anomalous that *C. edentula* var. *lacustris* and *C. edentula* var. *edentula* exhibited the longest maturation times. I suspect that the warm conditions of the growth chambers were somewhat inhibitory to seed germination and early seedling growth in these two taxa; in tests of seed germination at 20° and 30° C., I observed less germination at the higher temperature for *C. edentula* var. *edentula*. In studies on the

dune grasses *Ammophila breviligulata* (Seneca & Cooper 1971) and *Uniola paniculata* (Seneca 1972) with which *C. edentula* ssp. *edentula* and *C. edentula* ssp. *Harperi*, respectively, are associated, the researchers found seed germination and seedling growth in *Ammophila breviligulata* to be inhibited by higher temperatures and postulated this as a major environmental constraint on the southern distribution of this species. A similar constraint may operate on the northern *C. edentula* ssp. *edentula*; the southern *C. edentula* ssp. *Harperi*, like *Uniola paniculata* with which it is associated, may not be affected by higher temperatures. Interestingly, Tables 22 and 23 show *C. edentula* ssp. *Harperi* flowering earlier than *C. edentula* ssp. *edentula* of the Atlantic Coast.

Differences in maturation time were observed between Atlantic and Pacific coast *Cakile edentula* var. *edentula*. If real, the differences may reflect ecotypic differentiation in the naturalized *C. edentula* of the West Coast or, alternatively, constitute a founders' effect.

Cakile maritima from the Pacific Coast and from Norway had relatively short maturation times (32- and 35-day averages), shorter than that of *C. edentula* ssp. *edentula* from the Pacific Coast (36 days) or the Atlantic Coast (44 days). Barbour (1970a), however, reported 42 days to flowering for cultures of *C. maritima* grown in growth chambers but under somewhat different conditions than were employed here. A shorter growth cycle would contribute to the reproductive advantage which Barbour and Rodman (1970) postulated as the key to the replacement of *C. edentula* by *C. maritima* in California. The several hundred herbarium collections of these two species from the Pacific Coast which I have studied suggest, too, that flowering and fruiting in *C. maritima* is less seasonally defined than in *C. edentula*.

It is interesting that the taxa which I consider to be primarily autogamous (see section on breeding systems), *Cakile edentula*, *C. geniculata*, and, to some extent, *C. constricta*, take the longest time to flower. These grow over a wide latitudinal range; hence, the observed maturation times are not likely to be an expression of ecotypic adaptation to photoperiod, at least not in all these taxa. The differences between these species and the earlier-flowering, more allogamous taxa (e.g., *C. maritima* and *C. lanceolata*) may constitute differences in reproductive strategies. Faced with a developmentally imposed period of vegetative growth, those taxa with longer maturation times have responded to the need for adequate seed production with an increased emphasis on self-fertilization. Species with shorter maturation times can "afford" the risk of cross-fertilization (by insect pollination) to accomplish the same amount of seed production. This speculation may serve to direct further experimentation on the autecology of sea rockets, particularly on *C. edentula* and *C. maritima* which appear to employ different reproductive strategies and which are sympatric (and competitive?) on the Pacific Coast and in Australia.

Breeding Systems

Breeding system is defined here as a complex of morphological and behavioral characters of individuals or populations affecting the transmission of genetic material from one generation to the next. It encompasses floral morphology and phenology, pollination ecology, and genetic compatibility relationships. Aspects of fruit dispersal, seed germination, and seedling establishment, which also constitute the broad study of reproductive biology, are treated in the section on habitat and range. Concern with reproductive characteristics is taxonomically profitable since these features usually prove most reliable for classificatory purposes. Indeed, the species can be defined, at least theoretically, as a reproductive unit (Mayr 1963). Some (Ehrlich & Raven 1969) have argued that the biological species concept in its narrow emphasis on actual or potential gene flow ignores the considerable influence of natural selection, acting often antagonistically to gene flow, as a cohesive force in nature. Nonetheless, the concept provides a useful model for understanding variation in organisms (Dobzhansky 1972).

During three years of field work in North America and the West Indies, I made observations on populations of *Cakile edentula*, *C. constricta*, *C. geniculata*, *C. lanceolata* (except for subspecies *alacranensis*), and *C. maritima* ssp. *maritima*. Brief notes were made on the extent of fruiting in populations, on the kinds of insects seen visiting flowers (though whether actually pollinating them could not be determined), and on flower color and odor, time of opening, and duration of the blossom. These data can be combined with those on floral morphology and from plants grown in growth chambers to provide an overall view of the breeding systems in the various taxa.

In all the species studied the flowers typically open in the morning; cloudy skies may delay their opening for several hours. Blossoms usually last two to three days, and the petals close at least for the first night. The anthers dehisce, introrsely to slightly latrorsely, when the flower opens, at which time the stigma is just below or level with the four paired anthers which are usually exserted partially or wholly above the plane of the petal blades. In *Cakile edentula* the anthers often dehisce in bud just prior to flowering (Meehan 1892). Fresh flowers of *C. maritima* and *C. lanceolata* have a noticeable odor which is sweetly fragrant in the former (Salisbury 1952) but less sweet, though just as strong, in the latter. A conspicuous floral odor was noticed in cultivated plants of *C. arctica*. Flower color received considerable attention from Pobedimova (1964), but she failed to note the variation within species for this character. In all the species (with the possible exception of *C. arabica*) the color varies to some degree from white to lavender or pinkish purple although a particular species may have either white or predominantly lavender flowers. Within populations of *C. edentula*, *C. constricta*, and

C. maritima ssp. *maritima* I observed flower color which varied from white to lavender, violet, or pink-purple. Horovitz and Cohen (1972) also reported white and violet flowered plants of *C. maritima* in Israel. In populations of *C. lanceolata* and *C. geniculata* I found only white flowers although a few herbarium collections indicate that lavender petals may also be formed. Dr. Richard Howard (personal communication) reported two color morphs in the source population of collection 30 of *C. lanceolata* ssp. *lanceolata* in Puerto Rico. Petal color polymorphisms exist, therefore, in several taxa; within a population, however, aging may confound the situation since older white blossoms often turn purplish. Observations on herbarium labels of yellow or blue flowers in *Cakile* are almost certainly in error. The pale violet flowers of *C. maritima* in Israel have been shown to absorb a high level of near-wavelength ultraviolet light (350–400 mμ) more or less uniformly over the surface of the petals while the anther tips reflect UV (Horovitz & Cohen 1972). The flowers would thus present a target to UV-sensitive insects. A greater absorbtion of ultraviolet light was found in white-flowered forms of Israeli *C. maritima* (Horovitz & Cohen 1972).

Small black bees and a variety of flies and beetles were observed on flowers of *Cakile edentula* and *C. geniculata*. Small black bees, bumblebees, and honeybees in addition to a somewhat greater variety of Diptera and Coleoptera, as well as butterflies, were observed on the larger flowers of *C. lanceolata* and *C. maritima*. Knuth (1908) reported over 40 species of insects from flowers of *C. maritima* in northern Germany and also observed that flowers of this sea rocket were often half full of nectar in the "cup" formed by the erect sepals and petal claws. Probably only a small fraction of these visitors are effective pollinators, however, and, as Knuth also observed, are "as likely to effect cross- as self-pollination." Salisbury (1952) and Clapham, Tutin, and Warburg (1962) also reported a variety of insects as visitors of *C. maritima* in the British Isles.

Fruiting in natural populations was in general quite high in *Cakile edentula*, *C. constricta*, and *C. geniculata*. It varied more in *C. maritima* ssp. *maritima* although Barbour (1970d) stated that fruiting exceeded 90% in the populations he examined. I frequently observed plants of *C. lanceolata* with long racemes bearing few fruits or none at all. Herbarium material also suggests more erratic fruit set in the larger flowered taxa. This difference is paralleled by the results of spontaneous fruiting in plants grown under uniform environmental conditions (growth chamber with 16 hr daily photoperiod) as shown in Table 24. These results as well as those from artificial selfings of isolated plants confirm that all the taxa of *Cakile* tested so far are self-compatible. Even when artificially selfed, however, plants of *C. maritima*, *C. arctica*, and *C. lanceolata* ssp. *fusiformis* fruited poorly. For growth chamber plants grown from seed collected along the Pacific Coast, Barbour (1970d) also reported low values (4–12%) for spontaneous fruiting in *C. maritima*

TABLE 24. SPONTANEOUS FRUIT SET (NUMBER OF FRUIT/NUMBER OF FLOWERS) OF CAKILE GROWN UNDER UNIFORM ENVIRONMENTAL CONDITIONS.

Taxon	No. of cultures	No. of plants	% fruit set	Range
C. maritima ssp. baltica	2	15	0.6	0– 7
C. arctica	2	11	1.1	0– 13
C. lanceolata ssp. fusiformis	2	7	3.5	0– 5
C. maritima ssp. maritima	1	6	6.8	4– 10
C. lanceolata "Bermuda"	1	3	11.3	2– 19
C. lanceolata ssp. lanceolata	6	42	18.3	0– 68
C. geniculata	2	8	76.2	55–100
C. edentula ssp. Harperi	2	17	77.5	36–100
C. constricta	2	9	78.2	64–100
C. edentula ssp. edentula var. lacustris	2	14	82.0	65– 95
C. edentula ssp. edentula var. edentula	4	25	89.0	57–100

and a high value (94%) in *C. edentula*. The high incidence of spontaneous fruiting under cultivated conditions, the prolific fruit set observed in nature, and the formation of flowers with an incomplete set of petals strongly suggest considerable inbreeding in *C. edentula*. Inbreeding is probably great also in *C. constricta* and *C. geniculata* although the syndrome of autogamy in these species does not include a reduction in the number of petals (however, in a population in Brazoria County, Texas [collection 64] plants of *C. geniculata* with incomplete sets of petals but otherwise normal were occasionally observed).

In his review of self-incompatibility in the Cruciferae, Bateman (1955) listed *Cakile* as a self-sterile plant. It is probable that he had tested plants of *C. maritima* in this study. Bateman's criteria for such a designation included not only failure to set seed upon selfing but also finding much greater fruit set upon crossing than upon selfing. With such criteria, therefore, it is understandable that *C. maritima* would be classified as self-sterile; my studies would lead to the same conclusion. Nevertheless, I consider it misleading to designate the genus as self-sterile since no genetic barriers (at least, no strong barriers) exist to prevent self-fertilization.

Heslop-Harrison (1958) reported that plants in the Outer Hebrides identified as *Cakile edentula* (but see section on habitat and range) were gynodioecious. This condition has not been reported by others, nor did I find any indications of it during my field studies. The observations were perhaps made on aberrant plants. Gynodioecy is rare in the Cruciferae (Horovitz & Galil 1972).

To summarize data considered relevant to the breeding systems in *Cakile*, polygons were constructed along eight axes representing eight characteristics (Fig. 6): (1) petal length; (2) petal width [Table 2]; (3) lateral anther length [Table 4]; (4) relative nectary size; (5) average number of flowers produced along the main raceme [Table 10];

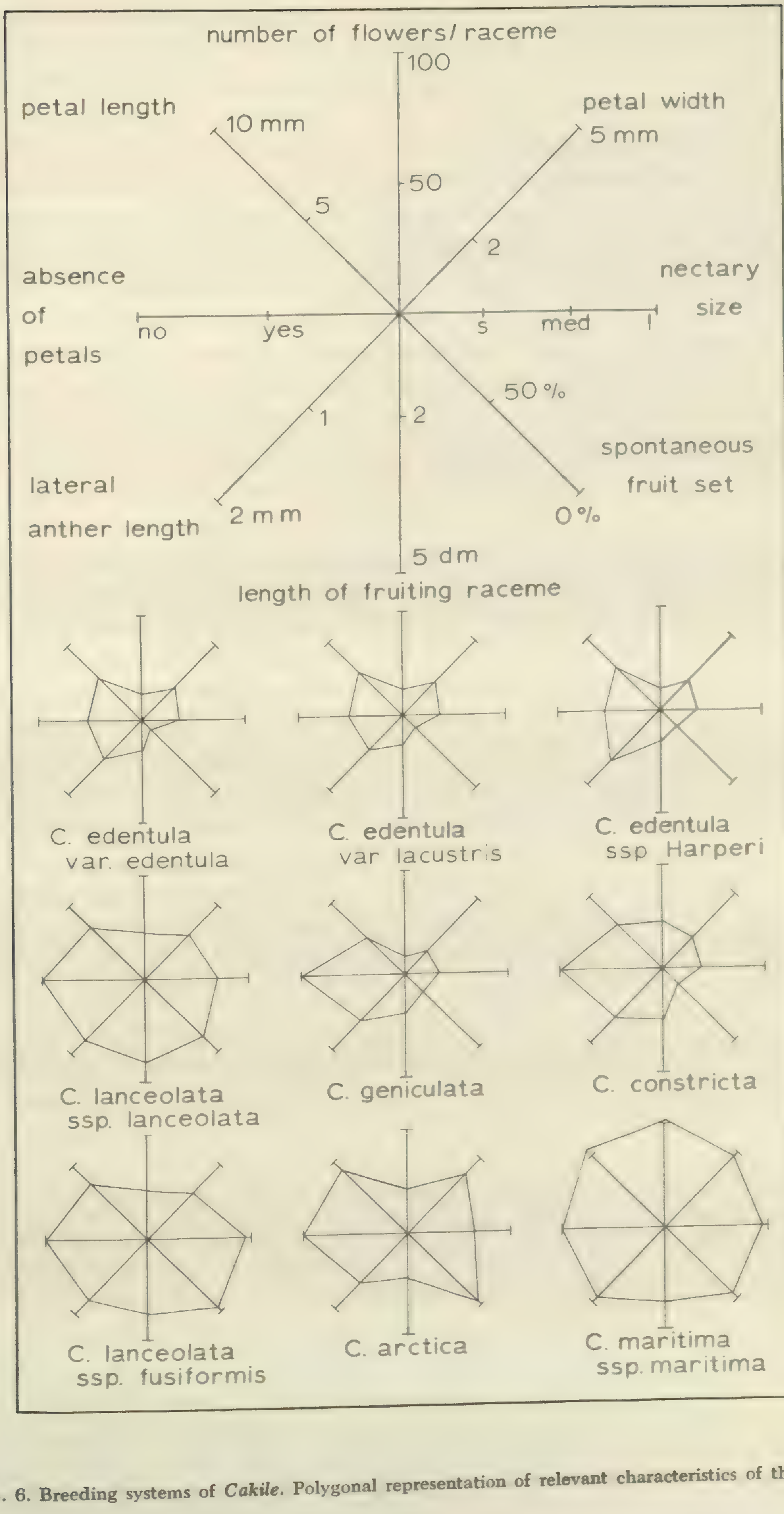


FIG. 6. Breeding systems of *Cakile*. Polygonal representation of relevant characteristics of the taxa.

(6) spontaneous fruiting [Table 24]; (7) average fruiting raceme length based on field observations and examination of herbarium collections; and (8) whether incomplete sets of petals were usually formed in nature. These polygons graphically depict what I consider to be primarily autogamous taxa (the small polygons of *C. edentula* and *C. geniculata*), primarily allogamous taxa (the large polygons of *C. maritima, C. lanceolata*, and *C. arctica*), and an intermediate *(C. constricta)*. In support of these distinctions are observations on floral odor, which is most noticeable in the allagamous taxa, and also on maturation time (see section on growth cycle), which is least in the allogamous taxa and greatest in the autogamous ones. Direct evidence of gene flow in populations of sea rockets is not available to test this apparent distinction between autogamous and allogamous taxa. However, the overall pattern is consistent with the facts of floral morphology and phenology, of the pattern of insect visitors, and of fruit set both in nature and under cultivated conditions.

The distinction between the autogamous *Cakile edentula* ssp. *edentula* var. *edentula* and the allogamous *C. maritima* ssp. *maritima* is particularly interesting since these two taxa have achieved great range extensions following their introduction by man into Australia and to the Pacific Coast of North America. Great dispersibility has certainly been a major determinant of the colonizing success of these taxa. In both regions the second species to be introduced, *C. maritima*, is replacing the earlier colonist. To explain this replacement, Barbour and Rodman (1970) pointed to a greater reproductive potential in *C. maritima*, and Barbour (1970d) summarized data on flower production in growth chamber collections of *C. maritima* from California and *C. edentula* from Oregon, demonstrating greater flower production in the former. Table 10, summarizing data on flower production from growth chamber studies, also supports this difference between the two species. Field and herbarium studies indicate that branching and consequent raceme production are at least as great in *C. maritima* as in *C. edentula*; hence, plants of the former can be expected to mature more fruits and seeds, assuming adequate pollination, than plants of the latter. The allogamous breeding system of *C. maritima* implies a requirement for insect pollinating activity to insure high fruit set and a consequent reproductive advantage over *C. edentula*. A variety of Hymenoptera and Diptera were observed as common visitors to the flowers of *C. maritima* on the West Coast; it appeared that fewer insects visited the less conspicuous flowers of *C. edentula*. An additional, phenological difference increases the reproductive superiority of *C. maritima*. This taxon, as Table 22 indicates, has a shorter maturation time than *C. edentula* from the West Coast. Plants of *C. maritima* came into flower sooner and lived longer than those of *C. edentula* under the growth chamber conditions employed. In 1969, field studies at Coos Bay, Beachside State Park, and Cape Lookout State Park, Oregon,

showed that a greater proportion of plants of *C. maritima* were in flower and/or fruit than of *C. edentula* in early August. I suspect that *C. maritima* also has a greater natural longevity than *C. edentula* although the record of herbarium collections from the West Coast does not indicate this. Field studies in local areas will be required to settle this point. Specimens of *C. edentula* have been collected in fruit in every month of the year whereas *C. maritima* has been collected in fruit throughout the year except in December and February (judging from the nearly 400 collections studied). The gap for *C. maritima* appears to be a vagary of collection since Barbour (1970b) reported plants in fruit in December at Bodega Bay, California, and stated that *C. maritima* there had one of the longest flowering seasons of any member of the flora—from March to October. Greater flower and fruit production, probably over a longer growing season, thus provides *C. maritima* with the reproductive advantage which accounts for its aggressive replacement of the highly self-fertilizing *C. edentula* on the Pacific Coast strand.

One can only speculate at present on the adaptive significance, if any, of the breeding systems in *Cakile*. Allard (1965) has demonstrated that the genetic variability of populations of inbreeders can be at least as great as that of populations of outbreeders. Indeed, the coefficients of variation for fruit length in *C. edentula* ssp. *edentula* and *C. maritima* ssp. *maritima*—presumably at opposite ends of the spectrum of breeding systems in the genus—are quite similar (see section on morphology and anatomy). The primarily autogamous taxon *C. edentula* may experience a shorter growing season and a more severe climate than allogamous taxa such as *C. lanceolata* and *C. maritima*, and consequently, autogamy may have been selected to assure adequate seed production in a harsher environment. *Cakile edentula* in particular must have been more drastically influenced by the Pleistocene glaciation than the more southern *C. lanceolata* or the Mediterranean *C. maritima*. By this line of reasoning the status of *C. arctica* appears anomalous. However, the syndrome of allogamy in *C. arctica* may reflect strong selective forces promoting outbreeding in a species comprising small insular or island-like populations where allogamy would offset the restrictions on genetic variability imposed by small population size (Carlquist 1966a,b). Autogamy in *C. geniculata* might appear to be dysfunctional since this taxon exists in a region which supports the more allogamous *C. constricta* and *C. lanceolata*. As noted in the section on growth cycle, however, *C. geniculata* has a relatively long maturation time; autogamy may have been selected to assure adequate seed production in plants confronted with a definite growing season and a long developmentally imposed vegetative stage. An alternative explanation involves an idea of Levin's (1971) that autogamy constitutes a mode of speciation in sympatric plants which reduces inter-race hybridization and hence allows divergent evolution. The range of *G. geniculata* overlaps that of both *C. constricta*

and *C. lanceolata;* autogamy might be expected to reduce the possibility of hybridization with these taxa and thus safeguard the genetic integrity, presumably adaptive, of *C. geniculata.* Autogamy thus becomes less the evolutionary dead end which many have assumed it to be (cf. Rollins 1967 for an appraisal) and more a mechanism of evolution in plants.

Hybridization

Areas of potential hybridization occur throughout the range of the genus *Cakile*: in southern Australia and the Pacific Northwest where the introduced *C. maritima* now grows with the earlier immigrant, *C. edentula*; along the Outer Banks of North Carolina where the northern *C. edentula* ssp. *edentula* gives way to *C. edentula* ssp. *Harperi* to the south; along the coast of Louisiana where *C. constricta* and *C. geniculata* grow intermixed; in Texas where *C. geniculata* and *C. lanceolata* ssp. *pseudoconstricta* occur sympatrically; and throughout much of southern Florida and the Yucatan Peninsula where the subspecies of *C. lanceolata* intermingle. In the Old World, the Aegean appears to be a region of potential hybridization between *C. maritima* ssp. *euxina* of the Black Sea and typical *C. maritima* in the Mediterranean (Pobedimova 1964; Ball 1964a). To the north, *C. maritima* ssp. *maritima* in the North Sea gives way through the Kattegat and Skagerrak channels to the aptly named *C. maritima* ssp. *baltica.* In these transition zones or areas of sympatry natural hybridization appears to generate the variations exhibited in these mixed populations. While hybrids have been identified by several botanists (Millspaugh 1900; Patman 1962; Eichler 1965), no study of hybrid populations has yet been published. To demonstrate that natural hybridization may occur in *Cakile,* I attempted crosses among several taxa in cultivation and also studied the distribution of characters in a number of population samples. The evidence, while circumstantial, suggests that natural hybridization is critically important in creating the patterns of variation present in many areas today and may have played a role in the evolution of certain taxa in the past.

Artificial crosses were attempted for ten different combinations involving *Cakile edentula* ssp. *edentula* and ssp. *Harperi, C. maritima* ssp. *maritima, C. geniculata,* and *C. lanceolata* ssp. *lanceolata* and ssp. *fusiformis* (Table 25). Plants were grown in insect-free growth chambers and, if serving as pistillate parent, were emasculated a day or two before pollination. *Cakile edentula* ssp. *edentula* and *C. geniculata* were not used as pistillate parents because of difficulties encountered in trying to emasculate their small buds and because frequently their anthers had dehisced in the bud prior to flowering. Since all the taxa of *Cakile* tested have proven to be self-compatible, accidental self-fertilization resulting from the emasculation process could have been a confounding factor. As a test for this in *C. lanceolata* ssp. *lanceolata* and ssp.

fusiformis, buds were emasculated as usual on several plants which were then left undisturbed in the growth chambers. In *C. lanceolata* ssp. *lanceolata* 15% of these flowers developed fruits, and in *C. lanceolata* ssp. *fusiformis*, 7%. These values are significantly lower than the values for fruit set observed for the artificially crossed plants, indicating that accidental self-fertilization was not a major problem. The same is true for *C. maritima*, where the value for fruit set resulting from the artificial crosses is significantly higher than what had been observed for spontaneous fruiting or from artificial selfings, indicating that accidental self-fertilization did not contribute in a major way to the observed fruit set. With *C. edentula* ssp. *Harperi* serving as pistillate parent, the values for fruit set resulting from the crosses were much lower than what has been observed for spontaneous fruit set in this taxon (ca. 80%). This may indicate the presence of an incipient genetic barrier to hybridization. However, damage to the gynoecium during the emasculation procedure may have reduced fruit set since the buds are quite small.

Tables 25 and 26 present various results for these artificial crosses. They include the percentage of fruit set on the pistillate plants (number of maturing fruits/number of flowers artificially pollinated), percentage of germination resulting from these crosses when grown under uniform

TABLE 25. PERCENTAGE OF FRUIT SET AND SEED GERMINATION IN ARTIFICIAL HYBRIDS

Hybrid	Fruit set on ♀ plants	No. of ♀ plants	Seed germination	No. of seeds from crosses
C. maritima ssp. maritima (69) × C. edentula var. edentula (96)*	85	20	71	76
C. edentula ssp. Harperi (24–2) × C. edentula var. edentula (34)	40	8	100	8
C. edentula ssp. Harperi (24–2) × C. lanceolata ssp. lanceolata (R-s.n.)	47	8	100	14
C. edentula ssp. Harperi (24–2) × C. lanceolata ssp. fusiformis (W–9138)	35	8	91	12
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. edentula var. edentula (26)	92	12	52	34
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. geniculata (25)	75	3	100	4
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. lanceolata ssp. fusiformis (W–9138–2)	68	11	77	31
C. lanceolata ssp. fusiformis (W–9138–2) × C. lanceolata ssp. lanceolata (R-s.n.-2)	73	18	96	56
C. lanceolata ssp. fusiformis (W–9138–2) × C. geniculata (25)	86	3	100	9
C. lanceolata ssp. fusiformis (W–9138–2) × C. edentula var. edentula (26)	71	3	100	9

Legend: *pistillate plant listed first; collection number given in parentheses.

TABLE 26. PERCENTAGE OF SPONTANEOUS FRUIT SET AND POLLEN VIABILITY OF F_1 HYBRIDS

Hybrid	Spontaneous fruit set of F_1 plants	No. of F_1 plants	Pollen viability of F_1 plants
C. maritima ssp. maritima (69) × C. edentula var. edentula (96)*	45**	7	–
C. edentula ssp. Harperi (24–2) × C. edentula var. edentula (34)	86	8	88
C. edentula ssp. Harperi (24–2) × C. lanceolata ssp. lanceolata (R-s.n.)	56	14	>90
C. edentula ssp. Harperi (24–2) × C. lanceolata ssp. fusiformis (W–9138)	80	11	>90
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. edentula var. edentula (26)	68	17	53
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. geniculata (25)	75	4	60
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. lanceolata ssp. fusiformis (W–9138–2)	56	17	>90
C. lanceolata ssp. fusiformis (W–9138–2) × C. lanceolata ssp. lanceolata (R-s.n.-2)	43	52	>90
C. lanceolata ssp. fusiformis (W–9138–2) × C. geniculata (25)	24	9	>90
C. lanceolata ssp. fusiformis (W–9138–2) × C. edentula var. edentula (26)	44	7	89

Legend: *pistillate plant listed first; collection number is given in parentheses; **fruit from artificial selfing.

environmental conditions, percentage of spontaneous fruit set (number of maturing fruits/number of flowers produced) in F_1 plants grown in growth chambers under uniform conditions, and percentage of pollen viability in these F_1 hybrids. To assess pollen viability, 100 grains from 4–11 F_1 plants were counted in methylene blue or acetocarmine and scored; aborted grains were much smaller than normal and did not take up the stain. It is evident from Tables 25 and 26 that viable seeds were produced from all the crosses and that the resulting F_1 hybrids were fertile, with a spontaneous fruit set ranging from 24 to 86% (in 69 × 96 F_1 plants, where spontaneous fruit set was very low, plants were artificially selfed to test their fertility, giving a value of 45% fruit set). No attempt was made to grow an F_2 generation.

The F_1 hybrids were generally intermediate between their parents in vegetative and floral morphology. Moreover, as demonstrated in the section on biochemical systematics, individual F_1 plants from the crosses *C. edentula* ssp. *Harperi* × *C. edentula* var. *edentula*, *C. lanceolata* ssp. *lanceolata* × *C. edentula* var. *edentula*, and *C. lanceolata* ssp. *fusiformis* × *C. edentula* var. *edentula* exhibited a seed isothiocyanate composition intermediate between their parents. Table 17 presents data on average petal length and width for F_1 hybrids from all the crosses. With two exceptions, the F_1 plants were consistently intermediate between their

parents in petal size. In two cases involving the small-flowered *C. edentula* ssp. *Harperi* as pistillate parent in crosses with *C. lanceolata*, the F_1 hybrids had slightly larger petals on the average than the larger-flowered, staminate parent. The two cases may constitute an example of heterosis.

These results from artificial crosses indicate that natural hybridization is a possibility for most of the taxa of *Cakile* if not for all. Crosses involving *C. constricta*, *C. arctica*, and especially *C. arabica* would complete our understanding of the genetic barriers, or lack of them, in this genus. Herbarium specimens of plants with intermediate morphologies and the patterns of character variation in mixed populations of sea rockets suggest that hybridization does occur in nature.

Eichler (1965) suggested that hybridization occurred in mixed populations of *Cakile maritima* and *C. edentula* in South Australia. Specimens he labeled as hybrids (*Eichler 12119*, AD, GH) do show some intermediate characteristics. However, *Eichler 14198* (AD, NSW), identified as a hybrid from its entire leaves, appears to be normal *C. maritima*. Plants of this taxon with entire leaves occur sporadically throughout its native range as well. Along the Pacific Coast of North America where the two species have also become naturalized, hybrids appear to be quite rare (Barbour & Rodman 1970). Dr. Dennis Anderson of Humboldt State College stated in a personal communication (1969) that he was unable to find any evidence of hybridization between the two in northern California. In the nearly 400 collections from the Pacific Coast studied, only three appear to be hybrids: *Schreiber 2185* (UC) from Marin County, Calif., *Tracey 18062* (NCU) from Humboldt County, Calif., and *Stuckey 1930* (OS) from Lincoln County, Oregon. No hybrids were detected during my own field work along the West Coast; in mixed poulations, plants could be readily identified as one or the other species. I attribute this lack of hybridization to the different breeding systems of the two taxa. The small-flowered *C. edentula* is probably highly self-fertilizing. However, *C. maritima* is primarily allogamous and probably dependent on insect activity for good fruit set. In their foraging activity, insects can be expected to consistently favor the larger, showier blossoms of this species.

Heslop-Harrison (1953, 1954) reported plants of *Cakile maritima* and *C. edentula* in the Outer Hebrides and a sterile hybrid between the two. The plants identified as *C. edentula*, however, are probably not this species as Clapham, Tutin, and Warburg (1962) pointed out. Rather, they may be *C. arctica*, native in Iceland and the Faeroes, or, as Ball (1964a) suggested, simply variants of *C. maritima*. The Icelandic plants have been treated as *C. edentula* by many botanists (Ball 1964a), and Heslop-Harrison (1953) speculated that the Hebridean and Icelandic plants were conspecific. Icelandic plants could have migrated by sea to the Outer Hebrides on the North Atlantic Current. Hybrids between *C. arctica* and *C. maritima* would be difficult to identify without fruiting material since the two are very similar in floral characters and even in

TABLE 27. AVERAGE PETAL LENGTH AND WIDTH (MM) OF PARENTAL AND F_1 PLANTS OF CAKILE

Hybrid	Pistillate Parent (N)*	Length	Width	F_1 Hybrids (N)	Length	Width	Staminate Parent (N)	Length	Width
C. maritima ssp. maritima (69) × C. edentula var. edentula (96)**	10	12.0	4.4	11	10.2	3.6	2	6.9	1.6
C. edentula ssp. Harperi (24–2) × C. edentula var. edentula (34)	10	8.9	3.6	6	8.7	3.0	10	7.8	1.7
C. edentula ssp. Harperi (24–2) × C. lanceolata ssp. lanceolata (R-s.n.)	10	8.9	3.6	10	9.8	5.0	10	9.0	4.8
C. edentula ssp. Harperi (24–2) × C. lanceolata ssp. fusiformis (W-9138)	10	8.9	3.6	10	10.4	5.0	10	10.1	4.8
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. edentula var. edentula (26)	10	9.0	4.6	10	8.0	3.7	4	6.8	2.0
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. geniculata (25)	10	9.0	4.6	4	8.0	3.8	10	6.4	2.2
C. lanceolata ssp. lanceolata (R-s.n.-2) × C. lanceolata ssp. fusiformis (W-9138-2)	10	9.0	4.6	10	11.1	5.8	10	11.3	5.8
C. lanceolata ssp. fusiformis (W-9138-2) × C. lanceolata ssp. lanceolata (R-s.n.-2)	10	11.3	5.8	10	10.6	5.8	10	9.0	4.6
C. lanceolata ssp. fusiformis (W-9138-2) × C. geniculata (25)	10	11.3	5.8	10	10.0	4.6	10	6.4	2.2
C. lanceolata ssp. fusiformis (W-9138-2) × C. edentula var. edentula (26)	10	11.3	5.8	10	10.0	4.5	4	6.8	2.0

*Number of plants measured; **Pistillate plant first and collection number in parentheses.

leaf morphology (considering the entire-leaved forms of *C. maritima*). A sterile F_1 hybrid would be unusual in view of my results from artificial crosses (albeit not between these two species).

On beaches of Lakes Michigan, Erie, and Ontario the native *Cakile edentula* var. *lacustris* occasionally grows intermixed with the rarer *C. edentula* var. *edentula*, which is most likely a recent introduction to the Great Lakes. Hybrids between the two appear to be rare. In Wisconsin, Patman and Iltis (1961) demonstrated a clear distinction in their material between the two varieties, and Dr. Hugh Iltis of the University of Wisconsin stated in a personal communication (1971) that hybrids were absent from that state. A few collections possibly of hybrid origin were noted among the nearly 400 collections studied from the Great Lakes region: *Bessey s.n.* (MSC), Muskegon Co., Mich. (upper fruit segment 9 mm long × 3.5 mm wide), *McVaugh 12633* (MICH), Manistee Co., Mich. (14 × 5.5 mm), and *Gross s.n.* (PH), Lincoln Co., Ontario (12 × 4.5 mm). It has not been determined, by attempting artificial crosses between the two varieties, whether genetic barriers to hybridization exist. The rarity of hybrids is probably conditioned by the strength of the autogamy in both taxa; in addition, their sympatry is presumably a recent phenomenon.

Along the Outer Banks of North Carolina *Cakile edentula* ssp. *edentula* gives way southward to *C. edentula* ssp. *Harperi*. A small sample (collection 40) and a mass sample (collection 41) from two populations in this region, when analyzed for seed glucosinolates, exhibited intermediate chemical profiles which may have resulted from hybridization (see section on biochemical systematics). Since synthesized F_1 hybrids were intermediate for seed glucosinolate composition, some support for hybridization in natural populations is adduced. The herbarium record indicates that hybrids are not common, however. Despite the absence of genetic barriers between the two subspecies, hybridization is, I think, restricted because of the presence of autogamy in both taxa.

Herbarium collections indicate that on the Atlantic Coast of Florida south to St. Lucie County *Cakile edentula* ssp. *Harperi* and *C. constricta* occasionally grow in mixed populations. Their sympatry is apparently not extensive. Five populations sampled in this region were found to be homogeneous, showing no evidence of hybridization. A few herbarium specimens appear to be hybrids: *Creager 417* (FLAS), Duval Co. (fruit 19 mm long) and *Arnold s.n.* (FLAS), St. Johns Co. (23.5 mm). In Volusia County and southward *C. lanceolata* ssp. *fusiformis* occurs and becomes the predominant sea rocket in Dade, Monroe, and Collier Counties. It grows with *C. constricta* in Indian River County (*Palmer 12* & *13*, GH) and perhaps in adjacent counties and may hybridize sporadically with that species (*Schallert 3997*, SMU, from Brevard Co.). Moreover, typical *C. lanceolata* occurs sporadically in the Florida Keys and north to Martin County although apparently never forming extensive populations.

Hybrids between it and *C. lanceolata* ssp. *fusiformis* were reported by Patman (1962) who stated that the hybrid "demonstrates many intermediate characters." However, the two subspecies are not markedly distinct, and hybrids between them would not be conspicuous. Sporadic collections in the Florida Keys and north to Pinellas County along the Gulf of Mexico approach *C. lanceolata* ssp. *alacranensis*. Millspaugh (1900) identified a specimen from Palm Beach County as a hybrid between "C. alacranensis" and "C. aequalis" (typical *C. lanceolata*) and remarked that such a hybrid was "a highly possible result, as the fruit of *C. alacranensis* could reach that locality on the current of the Gulf Stream which sweeps the shores of the Alacrans on its way to the Florida Keys." The specimen (*Webber 243*, MO) is *C. lanceolata* ssp. *fusiformis* which is indeed intermediate in fruit morphology between *C. lanceolata* ssp. *alacranensis* and the typical subspecies (Plate 1). *Cakile lanceolata* ssp. *fusiformis* may have arisen as a hybrid between *C. lanceolata* ssp. *alacranensis* and the typical subspecies, most likely in the area of the Gulf of Honduras from where it could be transported to the Florida Keys by the Gulf Stream. Its presence in Florida prior to the last glaciation is problematic since most if not all of southern Florida was periodically inundated during the Pleistocene (Flint 1971). Plants of *C. lanceolata* ssp. *fusiformis* breed true for floral and fruit characters under cultivation but show considerable variation in leaf form, from nearly entire to deeply

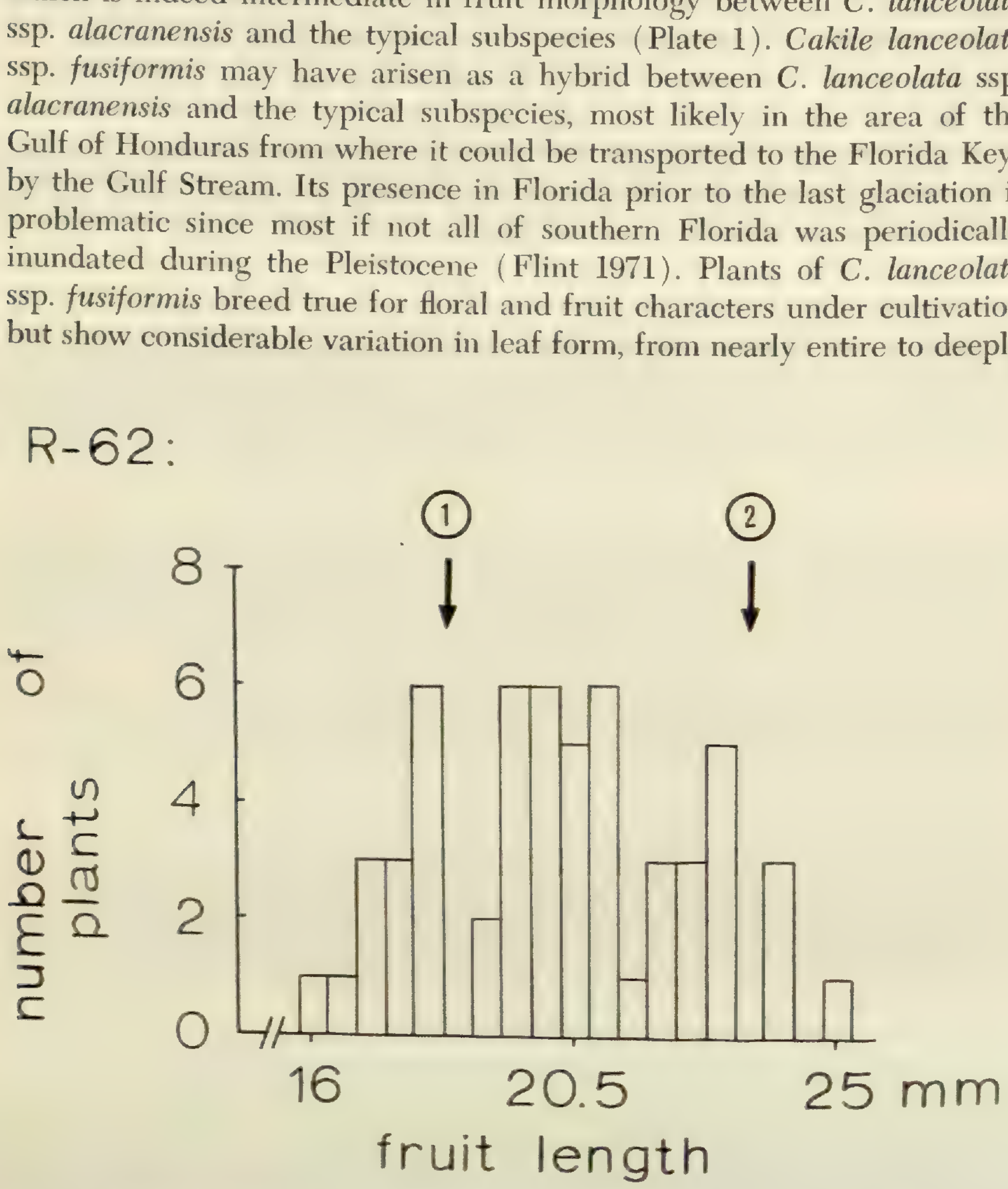


FIG. 7. Frequency histogram of fruit length in population sample R–62 (Grand Isle, Louisiana). Arrow 1. Average fruit length of *Cakile constricta;* Arrow 2. Average fruit length of *C. geniculata.*

pinnatifid. On the Gulf Coast from Lee to Pinellas counties, Florida, *C. lanceolata* ssp. *fusiformis* occasionally grows with the more common *C. lanceolata* ssp. *pseudoconstricta*, and hybrids may be expected between them. Peninsular Florida is a great meeting ground for sea rockets which presumably differentiated to varying degrees in other areas of the Gulf of Mexico and Caribbean and which subsequently gained a foothold on the more recently emergent Florida Platform. Repeated dispersals and hybridizations have blurred morphological differences which may not have been sharply discontinuous initially and have created a confusing array of forms reflected by the conflicting taxonomies of Millspaugh (1900), Small (1933), and Pobedimova (1964).

Hybridization also appears to contribute to the variability found in populations in Louisiana and eastern Texas where *Cakile constricta* and *C. geniculata* often grow sympatrically. Figures 7 and 8 present histograms of fruit length for 50-plant population samples of collections 62 from Grand Isle, Louisiana, and 64 from Brazoria County, Texas. These collections comprise a broad range of plants intermediate between the average values for fruit length for *C. constricta* (arrow 1) and *C. geniculata* (arrow 2). As noted in the section on morphology and anatomy, the difference in fruit length between these species is statistically significant; in the absence of hybridization, therefore, one would expect a bimodal distribution for fruit length in mixed populations of the two.

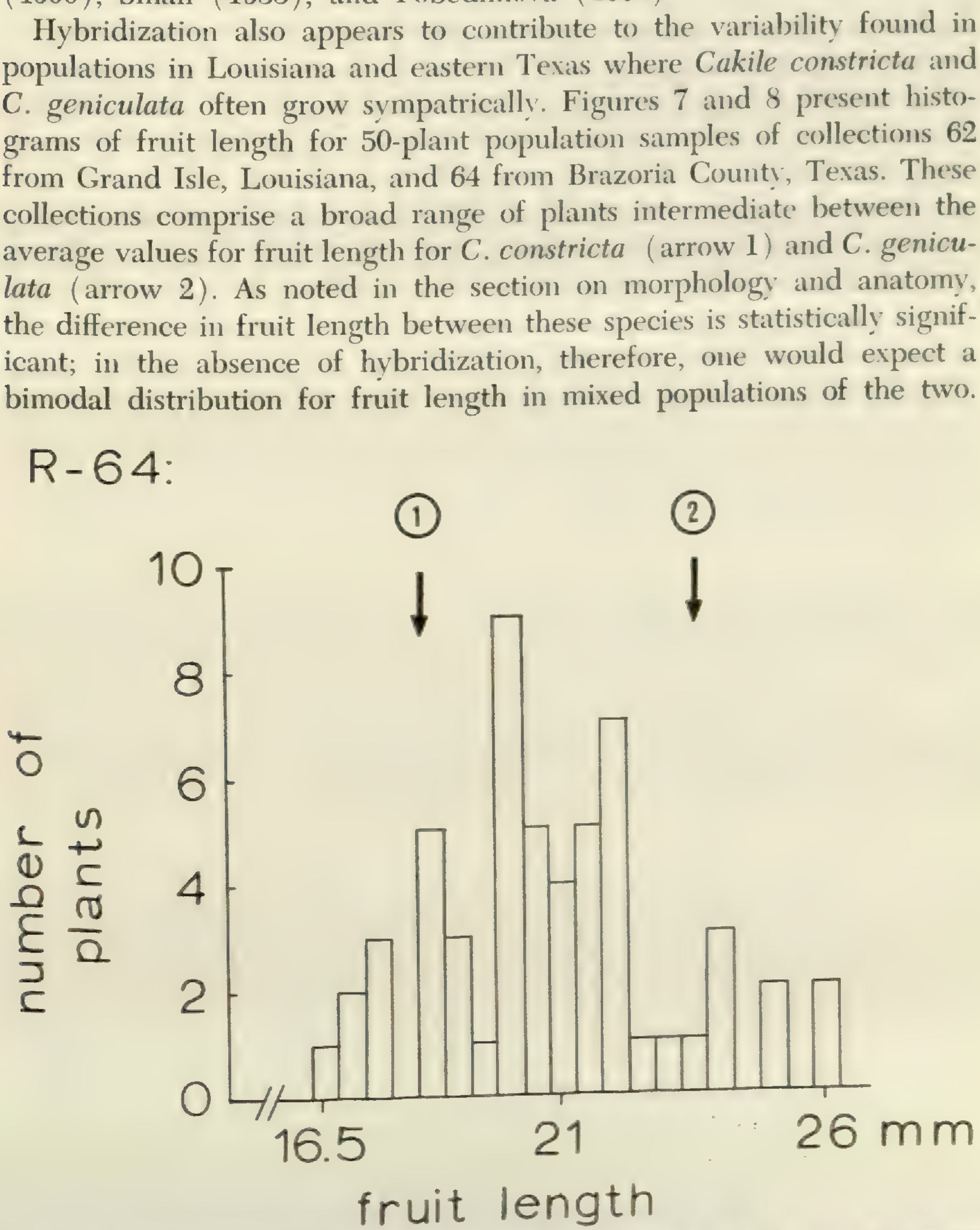


FIG. 8. Frequency histogram of fruit length in population sample R–64 (Brazoria Co., Texas). Arrow 1. Average fruit length of *Cakile constricta;* Arrow 2. Average fruit length of *C. geniculata.*

The observed distribution strongly suggests natural hybridization. Further west along the Texas coast, *C. geniculata* frequently grows intermixed with *C. lanceolata* ssp. *pseudoconstricta*, and a few herbarium collections (e.g., *Whitehouse 21169*, SMU, from Aransas Co.) suggest hybridization between the two.

The absence of genetic barriers to hybridization combined with great dispersibility have created a complex array of forms in the genus *Cakile*, especially on the shores of the Caribbean and the Gulf of Mexico. The present taxonomy surely oversimplifies a dynamic situation, one which is not likely to stabilize until the appearance of strong genetic or geographic barriers to intermingling. However, strong selective pressures may actually exist against genetic barriers in strand plants as Wilson (1965) suggested in a theoretical context. Colonizing plants which allow speciation to occur in effect create their own competitors; genetic differentiation may proceed to a point where hybridization results in sterile or stunted offspring, and consequently, effective population size and ranges are reduced. Despite the evident differentiation in sea rockets, therefore, there may be no selective advantage to genetic isolating mechanisms; since these plants are self-compatible, adaptive gene complexes can be preserved by inbreeding. Complex patterns of variability arising in part through frequent hybridizations may, therefore, remain an essential manifestation of the biology of the strand species of *Cakile*.

Habitat and Range

The species of *Cakile*, with one exception, are strand plants of the North Atlantic Ocean and adjoining bodies of water: the Baltic, North, and Barents seas north to Spitsbergen; the Mediterranean and Black seas; the Caribbean and Gulf of Mexico; and the Great Lakes of North America. The exception, *C. arabica*, is endemic to desert regions in a broad arc around the Persian Gulf but does not occur on the shores of the Gulf (*contra* Hultén 1945). Two strand species, *C. edentula* and *C. maritima*, have become widely naturalized along the Pacific Coast of North America (Barbour & Rodman 1970) and along much of the western, southern, and eastern shores of Australia. Sporadic collections outside the native ranges of these and other species undoubtedly represent cases of introduction by man in ships' ballast. Plants of *C. edentula*, for example, have been collected in the Azores and in New Zealand, and *C. maritima* has been found near major ports of eastern North America, Uruguay, Argentina, and New Caledonia. The ephemeral occurrence of members of this genus as ballast weeds may be more widespread than is presently documented by herbarium collections.

Where native and naturalized, the maritime species of *Cakile* typically grow on sandy beaches just beyond the reach of high tides in the pioneer zone of beach vegetation. The sea rockets commonly grow in thin, linear belts paralleling the shore, often in nearly pure stands at middle and

northern latitudes. They are frequently the vascular plants growing closest to the sea. The plants of the fresh-water Great Lakes occupy an analogous habitat, often growing, as Cowles (1899) observed, just above the influence of summer waves in nearly pure linear stands along the shore. Where dunes are developed, occasional sea rockets grow among the grass- and shrub-dominated dune vegetation though never as extensively as along the foredune above high tides. Rare, isolated plants have been collected in coastal salt marshes and along roadsides near a coast.

The strand habitat, called the middle beach by Cowles (1899), the storm beach by Johnson and York (1915), and the driftline by Chapman (1964), can be defined as the strip of shore above the influence of summer or tidal waves but washed by winter storm waves and thus corresponds to the berm of geologists (Bascom 1960; Schuberth 1970). Physical factors of the strand environment have been summarized by a number of workers (Cowles 1899, in a classic paper on the Lake Michigan sand dunes, Oosting 1954, Chapman 1964). For *Cakile maritima* in California, Barbour (1970a) considered the important factors to be saline ground water, shifting sand, dry surface soil, salt spray, high winds, and low soil nitrogen.

The poor water-retaining capacity of sand, high daytime temperatures, high winds, and high insolation combine to create an "edaphic desert," in Salisbury's words (1952), on the strand. The succulent nature of sea rockets has been interpreted as an adaptation for water storage in this xeric environment (Martin 1959) and alternatively as a response to salt spray (Boyce 1954) and to accumulation of salts from the sand (Uphof 1941). Controversy also exists as to whether the soil water in which sea rockets grow is saline (Johnson & York 1915; Barbour 1970a, who reported 450–1800 ppm. of soluble salts from strand soils near *Cakile*) or fresh (Kearney 1904; Boyce 1954; Martin 1959), becoming salty only when storm waves wash over the beach (Oosting 1954). The succulent character of the foliage appears to be genetically controlled since greenhouse and growth chamber plants, watered with ¼-strength Hoagland's solution, retain this feature. Because he found seed germination and seedling growth to be inhibited by low salt concentrations, Barbour (1970c) termed *Cakile* an "intolerant halophyte," which he distinguished from facultative and obligate halophytes. In laboratory experiments on *C. maritima*, Barbour (1970a) found the seedlings to be highly tolerant of salt spray, and from experiments on plants *in situ*, Martin (1959) stated that *C. edentula* was "completely tolerant to wind borne salt spray." These results weaken Veldkamp's (1971) assertion that sea rockets manifest no "typical special adaptations to the sandy beach." He also contested Barbour's (1970a) statement that low soil nitrogen characterizes the strand habitat and pointed out that sea rockets often grow over or near old driftlines where decaying organic debris

would enrich the soil. Barbour (1972) later published measurements of soil nitrogen made on the strand near Bodega Bay, California, which indicated low levels in the areas he sampled. Johnson and York (1915) stated without supporting evidence that *C. edentula* requires a well-drained soil, and Salisbury (1952) cited unpublished research demonstrating the poor growth of *C. maritima* in clay soils. The sand in which sea rockets grow presents challenges as well, however, since young seedlings may be buried in drifting sand and both young and old plants may be severely abraded by blowing sand particles. Older plants and clumps of seedlings frequently form mounds of sand, and this sand accumulation and the humus resulting from decay contribute to the initial formation of dune ridges and eventually of dune systems (Cowles 1899; Harshberger 1901; Salisbury 1952; Chapman 1964). *Cakile* is often among the first colonizers of blowouts in dunes (Erskine 1960) and of beaches recently swept by storms (Stoddart 1963, 1969). Thus, the sea rockets play a valuable though minor role in the reclamation of land at the edge of the sea.

Seed germination and its adaptive significance have also been investigated by a number of researchers. Becker (1912) and Barbour (1970a) reported similarly high germinability for seeds from shelled upper and lower fruit segments which had been recently collected. I also observed high rates of germination in greenhouse and growth-chamber collections and found that germinability was enhanced by nicking the seeds lightly to break the seed coat. The longevity of *Cakile* seeds has not been studied in detail although Binet's (1961) work on *C. maritima* suggests that the germinability of mature seeds increases over a period of several months and then declines. Ewart (1908) reported that a 67-year-old seed lot of *C. maritima* var. *americana* (= *C. edentula* var. *edentula*) and a 56 year-old seed lot of *C. maritima* var. *maritima* exhibited no germination. A very low rate of germination is observed when intact fruit segments are sown (Binet 1961; Barbour 1970a). Binet postulated seed dormancy in *Cakile* arising from a double inhibition: first, by the mature pericarp, an essentially mechanical inhibition resulting from its postulated impermeability to water, and second, by the seed coat, possibly a chemical inhibition although the nature of the inhibitor was not determined. Barbour (1972) reported that upper fruit segments which had been soaked in sea water had higher rates of germination than fruit segments that were not. He hypothesized that the sea water had weakened the pericarp and/or dissolved the chemical inhibitors in the seed coat. Furthermore, he suggested that such exposure to sea water imitated the natural dispersal conditions of upper fruit segments of *Cakile*.

The botanical literature has many references to the dispersal of *Cakile* fruits by water but I have found no references to actual observations of the fruits of *Cakile* at sea. Heatwole and Levins (1972) reported whole plants of *C. lanceolata* floating at sea near Puerto Rico; these were

green and, if in fruit, probably immature. Howard (1950) also mentioned that the whole plant of *C. lanceolata* is carried by sea currents, and he stated that land crabs dispersed the fleshy (immature) fruits of this species in the Bahamas. The fruit dimorphism of *Cakile* presumably reflects two different modes of dispersal (Millspaugh 1900, 1916; Zohary, cited in van der Pijl 1969; Harper, Lovell & Moore 1970): the upper, deciduous segments may be blown about the beach until lodged in the sand or carried out to sea and transported while the lower segments remain attached to the dead plant, eventually to be buried locally in the sand. The latter mode would explain the frequent occurrence of clumps of seedlings on small sand mounds observed during field studies and which Barbour (1970d, 1972) reported on the California strand. Dead plants may also be uprooted and blown about like tumbleweeds on the beach (Cowles 1899; Bowman 1918). The sea rockets thus appear adapted both to short-distance dispersal along the sandy beach and to long-distance dispersal at sea. Fruit dispersal in the desert species, *C. arabica*, has not been studied, but it is probable that the upper fruit segments of this species are wind-dispersed.

The buoyancy of the upper fruit segments and the viability of the enclosed seeds after exposure to salt water are two striking examples of *Cakile*'s adaptation to the strand habitat. Experimental studies of this aspect of the ecology of sea rockets are not numerous, however. The most extensive study was reported by the naturalist H. B. Guppy (1906, 1917). My own studies indicate that considerable variation in the capacity for floating exists within a species and, therefore, that the results from testing only a few fruits may not provide an accurate assessment of the potential for water dispersal. Figure 9 presents the results of my studies on flotation of the upper fruit segments and viability of the seeds following exposure to salt water in five species of *Cakile*. For these tests, 100–110 upper segments for each collection were first washed for five minutes in a commercial bleach, "Clorox" (to inhibit fungal growth), rinsed well with water, then placed in gallon jars of sea water (collected from Boston Harbor). The jars were shaken once daily (to simulate some wave action) and counts made each day of the number of floating segments for a period of ten weeks. To test for seed viability, 10 (usually sunken) fruit segments were removed at weekly intervals, rinsed well in water, and shelled; the seed coats were nicked to hasten imbibition and the seeds placed on wet filter paper in Petri dishes in the light at room temperature. The fruit segments used in these tests originated from population samples of 50 plants (in the case of collections 45, 58, 73, and 96) or from a few plants (collections 26 and B–103) or a single plant (65a). In collection R-s.n.-2, fruits from a few growth-chamber plants were used. In Figure 9 the percentage of upper segments still floating is indicated by broken lines and the percentage of seed germination by bars. It is evident that considerable variation exists in the buoyancy of the

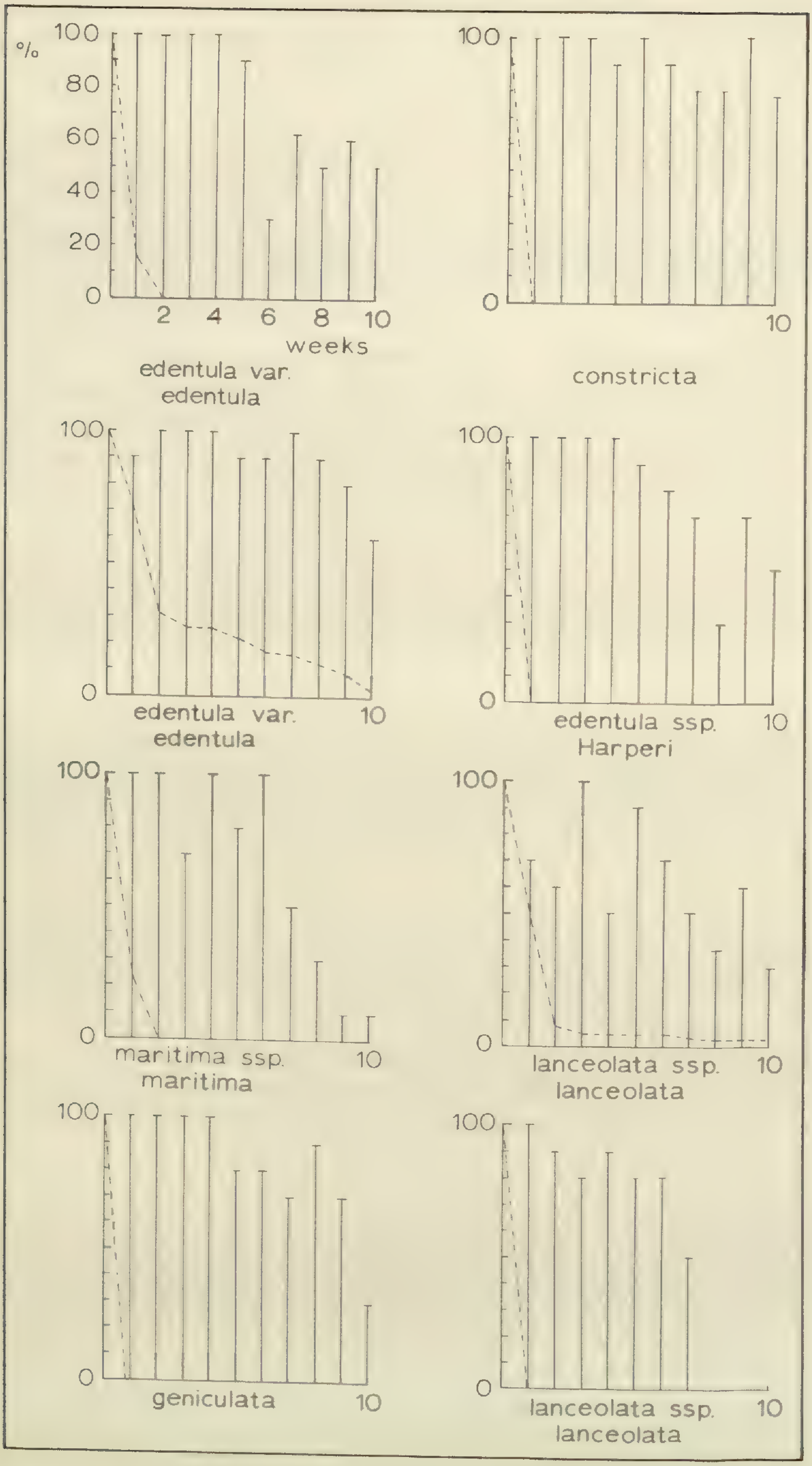


FIG. 9. Effect of sea water on seed germination and fruit flotation in *Cakile*. Percentage seed germination (bars) and percentage of upper fruit segments remaining afloat (broken lines).

fruits. For most of the collections the fruit segments had all sunk in one or two weeks; fruits of *C. edentula* ssp. *edentula* (96) and *C. lanceolata* ssp. *lanceolata* (R-s.n.-2), however, were still floating at the end of 10 weeks when the tests were concluded. The maximum floating time which Guppy found in his tests was for a collection of *C. lanceolata* (ssp. *lanceolata* most likely) from Jamaica. It is interesting that the longest floating times were found in two of the most widely distributed taxa.

The variation in buoyancy does not appear to be a simple function of the weight of the upper fruit segments or of the relative proportions by weight of the segment and the seed. This is evident from Table 28. Ridley (1930) stated that the variation in buoyancy was caused by variation in the amount of "spongy" tissue in the fruit as well as variation in

TABLE 28. AVERAGE WEIGHT OF UPPER FRUIT SEGMENTS (INCLUDING SEED) AND RATIO OF WEIGHT OF FRUIT SEGMENT (WITHOUT SEED) TO WEIGHT OF SEED IN CAKILE.

Taxon	Collection Number	Average weight (mg) of upper segment	Ratio
C. edentula ssp. edentula	96	31.4	2.0
C. constricta	58	11.5	2.2
C. edentula ssp. Harperi	45	46.0	2.7
C. geniculata	65a	30.6	3.9
C. lanceolata ssp. lanceolata	B-103	35.5	4.2
C. lanceolata ssp. lanceolata	R-s.n.-2	37.8	5.3
C. maritima ssp. maritima	73	44.2	5.5

the size of the suture on the articulating surface of the fruit segment. The importance of this latter feature had also been suggested by Guppy (1917). It is unknown whether these factors or others, such as the texture of the fruit or nature of the epidermis, account for the variation.

Seed viability, indicated by the bars in Figure 9, was retained by nearly all the collections even after 10 weeks in salt water. A decline in viability is evident after the fourth week, but only in collection B–103 of *Cakile lanceolata* ssp. *lanceolata* were the seeds completely killed by the sea water. Over 100 years ago the French botanist Charles Martins (1857) tested the viability of seeds of *C. maritima* with an ingeniously constructed box enclosing the fruits and attached to a buoy in the harbor of Sète on the Mediterranean Coast of France. After 45 days in the water the fruits were removed (no comment was made on whether they were floating) and planted; seeds from 13 of the 20 fruit segments of *C. maritima* tested (65%) germinated. The figure agrees well with the value I obtained for collection 73 of *C. maritima* ssp. *maritima* from California. Martins repeated his experiment on 20 upper fruit segments left for 93 days in the sea and found at the end of that time that all of the fruits had rotted, a result paralleling what I found in all the taxa tested.

Diaspores must manifest three properties for dispersal by sea currents

according to Lesko and Walker (1969): (1) the ability to float for several days; (2) the retention of seed viability after soaking in sea water; and (3) inhibition of germination by sea water. Regarding the third property (required to prevent germination at sea), I observed no germination from any of the fruits tested while they were in sea water. In addition, studies of the effects of sea water on germination have demonstrated that seeds of *Cakile* are inhibited by even low concentrations of salts (Barbour 1970a) and would probably not germinate under saline conditions. Thus, diaspores of *Cakile* possess the necessary characteristics for dispersal by sea currents and thereby manifest a sensitive adaptation to the strand environment.

Biotic factors affecting *Cakile* in the strand habitat are poorly known. Wilson (1907, 1908) reported that plants of *C. edentula* serve as hosts for the fungus *Albugo candida* which infects many Cruciferae. Flowers preserved in the field in FAA frequently contained small (up to 1.5 mm), white (larval) to brown (adult) thrips. It appeared to be the same species of thrips from all 35 collections where it was found, from the Atlantic and Pacific coasts of North America, the Gulf of Mexico, Jamaica, and Bermuda. A conspicuous infestation by small black beetles was observed in a mixed population of *C. edentula* and *C. maritima* near Coos Bay, Oregon, where many plants of both species bore damaged leaves, buds, and young fruits. Barbour (1970d) hypothesized that herbivory (by unknown agents) may be a factor in the exclusion of *Cakile* from the dune communities back of the strand.

Sea rockets have greatly extended their range within historical time as a result of their probable dispersal by man in ships' ballast. Where introduced and naturalized, they occupy a habitat similar to their native one. This is strikingly evident for *Cakile maritima* ssp. *maritima* which is abundant along the California coast and also naturalized in western and southern Australia—areas with a Mediterranean climate (Raven 1971). The herbarium record (discussed below) indicates that the rapid migration of *C. maritima* in California and its replacement of *C. edentula* there (Barbour & Rodman 1970) is paralleled by a similar migration of *C. maritima* in Australia and its replacement in South Australia and Victoria of the previously introduced *C. edentula*. The aggressive occupation of the strand habitat in these regions by the Old World *C. maritima* suggests that a similar naturalization might well occur in two other areas with a Mediterranean environment: the coast of Chile and the Cape region of South Africa.

The immigrant status of *Cakile edentula* in the Pacific region is not uncontested. Pobedimova (1963, 1964) accepted Heller's (1907) species, *C. californica*, as native, and, furthermore, she stated that the Australian material treated by her as *C. californica* was somewhat distinctive and might prove to be an indigenous species. I consider the Australian and West Coast plants to fall within the range of variation of the Atlantic

Coast *C. edentula* ssp. *edentula* var. *edentula* and find the herbarium and literature record a convincing proof of the migration and naturalization of the East Coast *C. edentula.*

The case for the introduced status of *Cakile edentula* on the Pacific Coast of North America has been presented by Barbour and Rodman (1970) and was made earlier by Jepson (1936). Our argument was basically historical and took for granted the taxonomic identity of Pacific and Atlantic coast *C. edentula,* concurring with the opinion of Hitchcock (1964). Here I hope to have presented sufficient evidence bearing on the morphology, glucosinolate chemistry, and reproductive biology of the two geographic entities to confirm Hitchcock's judgment. A few additional comments will round out the story.

The first accounts of *Cakile* by West Coast botanists are conflicting but suggest that the plants were initially limited in distribution although locally abundant in places. Behr (1888), for example, in the first published report of *Cakile* on the Pacific Coast, recorded it only from "Berkeley salt marshes." Greene (1891), however, remarked that *Cakile* was "common along sandy beaches about the Bay of San Francisco at West Berkeley, Alameda, etc., also at Half Moon Bay; doubtless not rare on the coast and probably indigenous." This last comment was disputed by Katharine Brandegee (1892) who treated *C. edentula* as an alien and observed that it occurred "about the shore sparingly from Black Point to the outlet of Lake Merced, and very abundant a short distance south of it." LeRoy Abrams did not record *Cakile* in his early floras of Los Angeles and vicinity (1904, 1911, 1917) although it had been collected in nearby Orange County in 1907 (*Davidson 1770,* DS) and in Ventura County in 1916 (*Eastwood 5024,* CAS). In their flora of the Northwest Coast, Piper and Beattie (1915) noted that *C. edentula* was "very rare along the seacoast." Relevant comments on herbarium labels are scarce, but a revealing one on the collection of *E. A. McGregor s.n.* (DS) from Pacific County, Washington, in 1907 reads: "this specimen extends dist[ribution] from Golden Gate."

Eastern botanists of the period, for example Robinson (1895) and Millspaugh (1900) who monographed the genus, believed the sea rockets were introduced. But in 1922 Fernald published his new combination, *Cakile edentula* var. *californica* (Heller), and provided a plausible rationale for the existence of a native West Coast taxon by invoking the argument of a Pleistocene disjunction in a previously boreal distribution. No fossil record of *Cakile* exists apparently to test such a hypothesis, and the genus is absent from the Alaskan and Canadian Arctic and from Greenland [the report of *C. edentula* from Hudson Bay was stated by Scoggan (1957) to be a misidentification of a young plant of *Chrysanthemum arcticum,* the leaves of which superficially resemble those of the sea rocket]. Fernald's idea undoubtedly influenced Hultén's acceptance of the West Coast plants as native (1936, 1968) although he

chose to treat them as *C. edentula* ssp. *californica* (1945). While accepting Fernald's combination, Jepson (1925) maintained that the taxon was introduced and provided a brief historical argument for his opinion in 1936. That same year, George Neville Jones made the interesting observation that "it is perhaps significant that the Makah Indians [of Washington] have neither name nor use for the plant." Heller (1907) and Fernald (1922) considered the West Coast plants to be somewhat more robust than their East Coast congeners, a characteristic which, if valid at all, is probably environmental (my growth-chamber collections showed no vegetative differences). Fernald (1922) remarked that the "fruits are in form essentially identical with those of many eastern specimens" but maintained that the two could be distinguished by the presence of small teeth on the articulating surface of the lower fruit segment of West Coast plants. This feature is encountered in East Coast material, however, and it varies within cultures from both coasts grown under uniform environmental conditions (Calder & Taylor 1968). Pobedimova (1964) conceded that it was difficult to distinguish East and West Coast plants and sometimes impossible without knowledge of their geographic provenance. While the plants of both coasts are virtually indistinguishable, a perfect identity can not be expected; ecotypic differentiation or a founders' effect could obscure their common origin. The tendency toward slightly larger petals in West Coast collections of *C. edentula* (see section on morphology and anatomy) may reflect such phenomena.

The relatively rapid replacement of *Cakile edentula* by *C. maritima* along the California coast, following the latter's introduction around 1935, has been documented by Barbour and Rodman (1970). The phenomenon has also been adumbrated in a number of recent floristic works on California where the authors have noted the greater abundance of *C. maritima* —for example, for Marin County (Howell 1949, 1970) and for San Luis Obispo County (Hoover 1970). The argument for a reproductive advantage in *C. maritima* as an explanation for this replacement, proposed by Barbour and Rodman (1970) and Barbour (1970d), is developed here in the section on breeding systems.

In Australia a remarkably parallel sequence of events occurred, with the introduction and naturalization of *Cakile edentula* from the Atlantic Coast of North America followed by the introduction and spread of the Old World *C. maritima*. Both species migrated widely and rapidly along the coast of temperate Australia, establishing extensive ranges which currently overlap on the shores of the states of South Australia and Victoria. In this zone, plants with intermediate characters suggest that some hybridization is occurring. The situation is a dynamic one, and a similar process of replacement of *C. edentula* by *C. maritima*, now nearing completion in California, appears to be underway on the Australian littoral.

The first collectors on the continent found no *Cakile* on its shores; at

least, Bentham did not record the genus in his *Flora Australiensis* (Bentham & Mueller 1863) although he studied all the major collections of such early visitors as Banks and Solander, Robert Brown, James Drummond, Allan Cunningham, and J. D. Hooker. Localities where *Cakile* now grows had been visited (e.g., the famous Botany Bay area, Spencer Gulf, the mouth of the Swan River), and coastal plants with which *Cakile* is now associated were listed by Bentham: *Spinifex hirsutus* and *S. longifolius, Scirpus nodosus, Sporobolus virginicus, Lepidosperma gladiatum,* and *Poa australis*. The lack of an early record did not result, therefore, from a lack of botanical collecting in suitable habitats.

The earliest collection of *Cakile* from Australia which I have seen is of *C. edentula* ssp. *edentula* var. *edentula*, made by Ferdinand von Mueller (*s.n.*, GH,K,MEL,NY) on Phillip Island, Victoria, near the port of Melbourne, in 1863. It was this collection on which Hemsley (1879) based the first published report of *Cakile* in Australia (as *C. maritima*). And it was probably this collection or some other very early one of *C. edentula* to which Ridley (1930) referred when he wrote: "*C. maritima* [sic] was in Australia before 1867. It was no doubt transported there in sand ballast." The MEL sheet, #1004009, bears the comment (not apparently in Mueller's hand): "known there wild since 20 years." It is possible, therefore, that *C. edentula* was introduced as early as the 1840's near Melbourne, a major port, in ballast. American seal hunters from New England, enroute to Kangaroo Island, sailed the area repeatedly in the early 19th century (Dr. Elizabeth Shaw, personal communication; *contra* Sims 1968). A later specimen sent to Mueller by John Mason of Belfast, western Victoria (*s.n.*, MEL #1004017), includes his letter of 18 September 1876 which reads in part: ". . . its first appearance was about three years since and it continues to spread through the sand down to the margin of the sea and promises to cover in a short time the whole of the sand patches on the coast." In 1870 W. Woolls sent Mueller a specimen of *C. edentula* (*s.n.*, MEL #1004032) collected from Manly Beach near the port of Sydney, New South Wales. It has been collected repeatedly from the state since then and was reported (as *C. maritima*) by Moore and Betche (1893) and by Maiden and Betche (1916). In 1881 R. Tate collected *C. edentula* at D'Estrees Bay on Kangaroo Island (*s.n.*, AD), which is apparently the first collection from the state of South Australia. Tate (1890) recorded the sea rocket in an early local flora of the state (again as *C. maritima*, in accord with prevailing custom), and Black (1909) also reported "*C. maritima*" (clearly *C. edentula* from his figure) and commented that it was ". . . accepted by some botanists as native, but not recorded in Australia until 1869 [sic] when it was found on the shores of Port Phillip Bay and French Island." In 1893 J. Bufton (*s.n.*, MEL #1004025) and J. H. Maclaine (*s.n.*,MEL #1004022) extended its known range to Tasmania with collections from Port Davey and Clarke Island, respectively. In 1898 G. King (*s.n.*, NSW) collected *C. edentula*

on Lord Howe Island where it has apparently persisted. The earliest collection from Queensland I have seen is *C. T. White 1680* (BRI,NSW) from Stradbroke Island, near Brisbane, in 1922, and the earliest from New Zealand may be *Philson, Doore, and Earle 340* (GH), collected on Stewart Island in 1935. [I have not seen material, however, from New Zealand herbaria; Pobedimova (1963) mapped *C. maritima* in New Zealand, but I suspect this is in error for *C. edentula.*] Recently, *C. edentula* has penetrated into Western Australia; *D. E. Symon 4685* (AD,NSW) and *Parsons 8* (AD), collected in 1967 from Eucla near the state border with South Australia, are the only specimens of this taxon I have seen from Western Australia. Sims (1968) reported *C. edentula* at Esperance in 1950, but I suspect that he mistook forms of *C. maritima* with poorly developed lateral horns on the lower fruit segments (common in Western Australia, e.g., *Eichler 20300*, AD,GH, from Esperance) for it. The herbarium record thus reveals a progressive migration of *C. edentula* outward from the state of Victoria, east into New South Wales, to Lord Howe Island, and eventually north into Queensland, west to South Australia and recently into Western Australia, south to Tasmania and New Zealand. Whether dispersed on sea currents or transported in ballast, *C. edentula* rapidly colonized southeastern Australia while it achieved a similar success, nearly contemporaneously, on the Pacific Coast of North America.

In Western Australia where *Cakile edentula* was yet unknown, the second invader, *C. maritima*, appeared. The earliest collection I have seen is *R. Helms s.n.* (PERTH) from Fremantle, a suburb of Perth, made in 1897, some 30 years later than the first collection of *C. edentula* in Australia and over 50 years later than Lindley's (1840) *Sketch of the Vegetation* of the region in which he reported the only Cruciferae as *Lepidium* and *Stenopetalum.* As with its migrating North American congener, this second immigrant most likely arrived in ships' ballast. Additional collections of *C. maritima* were made in the early 1900s, all in Western Australia, while *C. edentula* was colonizing Victoria, New South Wales, Tasmania, and, to a limited degree, South Australia. The first published accounts of *C. maritima* appeared in 1921 (cited in Sauer 1965) as incidental observations on the flora of Western Australia.

In 1918 *Cakile maritima* ssp. *maritima* was collected, perhaps for the first time, in South Australia at Kybybolite (*Andrew s.n.*, AD). Additional collections of both species were made in the 1920s in South Australia, including a specimen (*Cleland s.n.*, AD, 1924) which appears to be a hybrid of the two. Black (1924) early recorded the Old World species ". . . with pinnatipartite leaves and the lower article with two short spreading horns . . ." in his flora of the state, and Black (1935) and Cleland and Black (1941) reported "*C. maritima* var. *pinnatifida*" from Kangaroo Island where only *C. edentula* had been found previously. *Cakile maritima* then migrated farther eastward into the state of Vic-

toria. The collection *Tagdell s.n.* (MEL) from Beaumaris, near Melbourne, made in 1922, is the earliest I have seen of this species in Victoria. Again, the herbarium record (ca. 300 collections from Australia) suggests a progressive migration: Western Australia, 1897; South Australia, 1918; Victoria, 1922. In his flora of Victoria, Ewart (1930) recorded a single species of sea rocket, referring to the then well-collected *C. edentula* as ". . . *C. maritima* . . . the Victorian plant belong[ing] to the variety *edentula* (*C. edentula* Bigel.) . . . First recorded from Port Phillip and French Island in 1869." He was apparently unaware that true *C. maritima* had invaded the state. I have seen no specimens of *C. maritima* from Tasmania; but Black (1948) reported it there, and Curtis (1956), after recording the presence of *C. edentula*, stated: "*C. maritima* Scop., native in Europe and introduced in temperate Australia, may also be found in Tasmania."

Migrating into South Australia and Victoria, *Cakile maritima* came into contact with the earlier introduction, *C. edentula*, and must have coexisted with it for some time and perhaps hybridized with it to a limited extent. The herbarium record indicates, however, that *C. maritima* has replaced *C. edentula* in these two states as it did in California. This phenomenon has not been recognized in the literature but it is clearly supported by the record of collections in Australian herbaria. Of the 71 collections made in the last three decades in South Australia which I have seen, only two are of *C. edentula*. Of the 19 collections I have seen from Victoria, made in the same period, only one is of *C. edentula*. As in Western Australia (Sauer 1965), *C. maritima* is common and apparently abundant along the South Australia littoral (Sims 1968). *Cakile edentula*, however, was probably never very common there. The two may still coexist in places; Eichler (1965) suggested that the two were hybridizing in South Australia, but the opportunities for this would appear to be decreasing. The replacement is most dramatic in Victoria where an early record of *C. edentula* over several decades has given way to an almost exclusive record of *C. maritima*. While I have not seen specimens of *C. maritima* from New South Wales, the species has recently migrated to that state. In a personal communication (1972), Dr. R. H. Groves of the Division of Plant Industry of the CSIRO wrote: "As far as we can understand, what is happening on the N.S.W. south coast at the moment is that the first plants of *C. maritima* have arrived (presumably from Victoria where it occurs commonly). Only *C. edentula* occurs on N.S.W. and Queensland beaches at present. Thus we may be witnessing the interesting ecological situation which occurred in California, on the basis of your herbarium evidence, some 35 years ago." A competitive struggle analogous to that on the strand of the Pacific Northwest appears to be developing in New South Wales. It is surely an unstable situation, inviting more extensive field studies of the population dynamics of these two colonizing species.

The same two species have been collected from other areas outside their native ranges, but nowhere else have they duplicated the successful colonization of such vast stretches of sandy shore. In eastern North America, an area of indigenous sea rockets, *Cakile maritima* has been collected from ballast ground near the ports of New York, Philadelphia, Norfolk, Mobile, and Wilmington. Dense populations may build up locally (Brown 1879), often with the native sea rocket intermixed (Ahles 1951), only to disappear after a few years. *Cakile maritima* has also been collected near major ports in Uruguay and Argentina (Hauman 1925; Rollins 1940), but whether appearing intermittently as a ballast weed or persisting in stable populations is unknown. The reverse invasion of the Old World by the North American *C. edentula* has also occurred. The species has been collected from the English Channel Islands (Millspaugh 1900) and from the Azores (Millspaugh 1900), where, according to Guppy (1917), it was found as early as 1842. Reports of *C. edentula* in northern Scotland and the Outer Hebrides (Wilmott 1949; Allen 1952; Lousley 1953; Heslop-Harrison 1953a,b, 1954, 1955, 1956, 1958; Löve & Löve 1956) have resulted from mistaken identifications (Clapham, Tutin & Warburg 1962; Ball 1964a), understandable since Icelandic plants were usually treated as *C. edentula* at this time (Wilmott 1949; Heslop-Harrison 1953a). If not forms of *C. maritima*, as Ball (1964a) suggested, these plants in northern Scotland are likely to be of *C. arctica*, transported by sea currents from the Faeroes or Iceland. The occurrence of true *C. edentula* is sporadic in the Old World.

Cakile edentula ssp. *edentula* var. *edentula* has also invaded the Great Lakes where the closely related *C. edentula* ssp. *edentula* var. *lacustris* is native. The two grow intermixed on the lake shores and, except for rare hybrids, maintain their identity. The more widespread native variety probably evolved on the shores of the ancestral Great Lakes following the Wisconsin glaciation while the rarer typical variety probably invaded in historical times, perhaps in ballast. The recognition of two taxa in the Great Lakes area dates back at least to Millspaugh (1900) who treated them as *C. edentula* and *C. americana* Nutt. Nuttall based his species concept on material from both the Atlantic Coast and the Great Lakes (from which material a lectotype should be designated, but I have not seen his specimens; and whether lectotypified by an Atlantic Coast plant or one from the Great Lakes, the name would remain in synonymy). His name was widely used by those unaware of Bigelow's earlier name for the East Coast species or by those who chose to distinguish, at specific rank, between Northeastern plants with short- or long-beaked upper fruit segments. Beak length varies within Atlantic Coast *C. edentula* ssp. *edentula* but on the average is shorter than in Great Lakes material (see section on morphology and anatomy). Fernald (1922) also recognized two taxa in the Great Lakes region (the varieties accepted here), but his criterion for distinguishing the two—the presence of teeth on the articu-

lating surface of the lower fruit segment—is unreliable.

Of the 394 herbarium collections of *Cakile* studied from the Great Lakes, 30 (7.6%) were clearly *C. edentula* var. *edentula*, and four (1.0%) were probably hybrids. I have seen no collections of the typical variety from Lake Huron or Lake Superior, and the herbarium record suggests that it occurs only sporadically on the beaches of Lakes Michigan, Erie, and Ontario. Most of the collections (26) are from the southern end of Lake Michigan, usually in the vicinity of Chicago. Even here, however, typical *C. edentula* is less common than the native variety. Swink (1969), for example, stated: "Most of our material is referable to var. *lacustris*, although the type does occur . . ."; and in his "Flora of the Indiana Dunes," Peattie (1930) remarked that ". . . the typical species is found elsewhere on the shores of Lake Michigan, but no specimens from the Indiana coast have been seen." Deam (1940), likewise recorded only *C. edentula* var. *lacustris;* however, I have seen a few collections of typical *C. edentula* from the Indiana shore (*Umbach 11744*, WIS; *Pennell 6448*, NY). Patman and Iltis (1961) imply that it is more common along the Wisconsin shore of Lake Michigan, but relative to the native variety it appears to be much less abundant.

The sporadic occurrence of *Cakile edentula* var. *edentula* in the Great Lakes region suggests that it is a recent introduction. It might have entered the area as a ballast plant following the opening of the Erie Canal in 1825. Unfortunately, I have encountered no specimens of either variety antedating that event. Nuttall's Great Lakes material must have been var. *lacustris*; at least, his name, *C. americana*, was widely adopted for long-beaked specimens. The earliest collections from the Great Lakes I have seen, 1838, are of *C. edentula* var. *lacustris* (*Wright s.n.*, MICH; *Clinton s.n.*, F,MICH,MSC,NY). However, the collection of I. A. Lapham (*s.n.*), made in 1841 at Milwaukee, includes both *C. edentula* var. *lacustris* (F, MEL,MO,NY,RSA,WIS) and *C. edentula* var. *edentula* (PH). It is by no means certain that these specimens represent the same gathering in the same year. The early introduction of typical *C. edentula* at Milwaukee, however, might explain its more common occurrence along the Wisconsin shore. In 1843 Torrey cited a specimen of *C. edentula* var. *edentula* collected by P. D. Kneiskern (*s.n.*, NY) from Lake Ontario. The herbarium record, therefore, provides no clear indication for the recent migration of typical *C. edentula* into the Great Lakes region. Its status as an alien must remain an hypothesis, but one which is most consistent with the view that the var. *lacustris* evolved in the Great Lakes area as a geographically isolated entity.

Evolution

No fossils of *Cakile* are known (Pobedimova 1963). In the absence of a physical record of its evolutionary history, a phylogeny of the group can only be reconstructed by inferences drawn from structural and

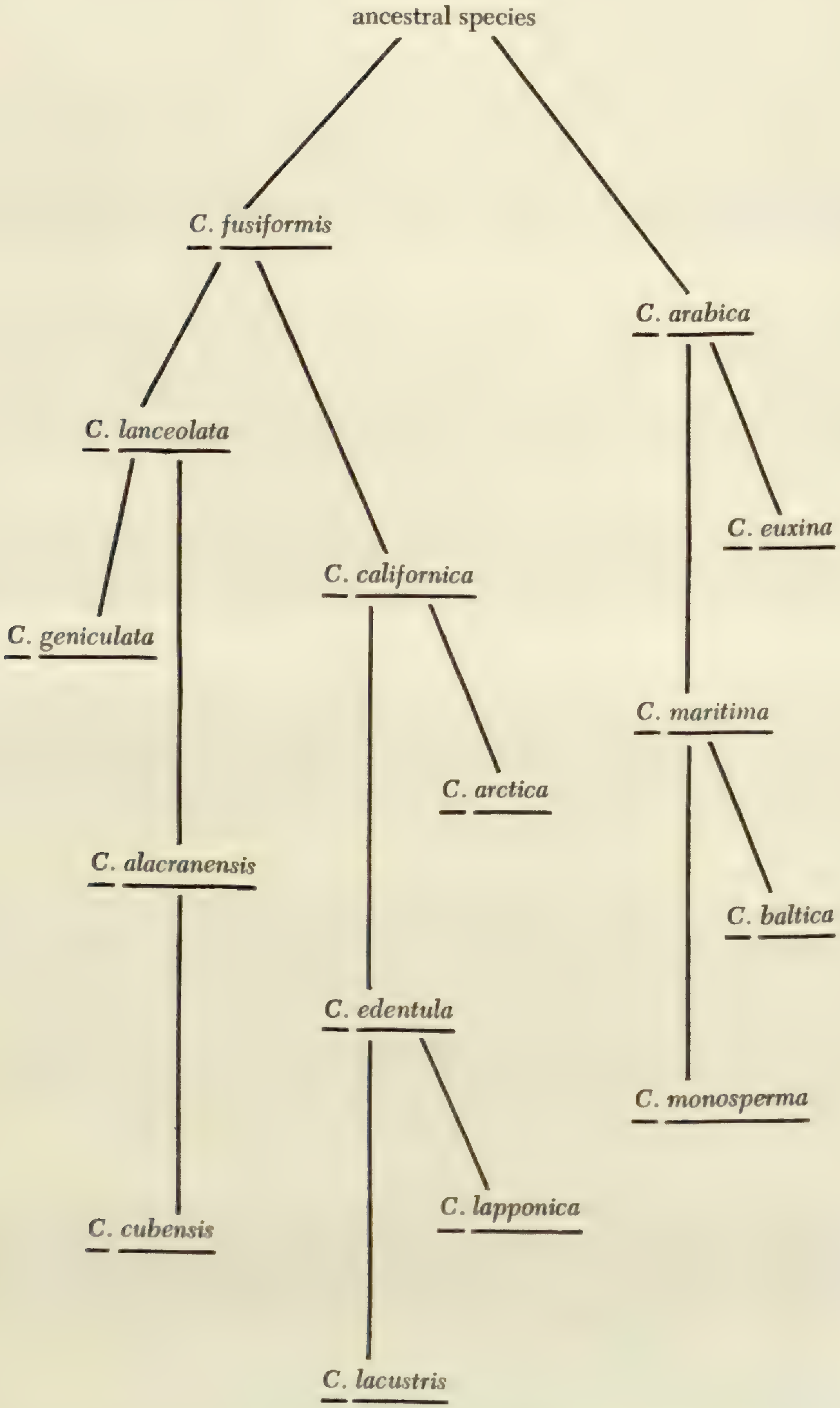


FIGURE 10. PHYLOGENETIC SCHEME OF CAKILE (POBEDIMOVA 1963).

functional similarities, interpreted within a geological framework relevant to the present distribution of the species and their presumed age. Such a reconstruction is attempted here by applying the evolutionary mechanism of speciation by geographic isolation to the biology of *Cakile* as now understood.

In her monograph of the genus, Pobedimova (1963) discussed the probable evolution of the species and summarized her ideas in a phylogenetic "scheme" reproduced here as Figure 10. The genus was considered to have been derived monophyletically from *Erucaria*, with an ancestral species referred to as Tethyan in age and distribution. This presumably widespread Tethyan ancestor diverged into two archaic species, *C. arabica* in the Old World and *C. fusiformis* in the New, and these eventually gave rise to an additional 13 species, probably since the Pliocene. Speciation by geographic isolation was emphasized as the primary mode of differentiation in *Cakile*. This was manifested in the Old World by the evolution of *C. euxina* in the Black Sea, *C. maritima* in the Mediterranean, *C. baltica* in the Baltic Sea, and *C. monosperma* in Western Europe, in that chronological sequence. In the Americas the tropical section Xiphocakile *sensu* Pobedimova (1964: *C. fusiformis, C. lanceolata, C. geniculata, C. alacranensis*, and *C. cubensis*) was stated to have evolved in response to fluctuating sea levels. From this primitive section, the northern section Integrifoliae *sensu* Pobedimova (*C. californica, C. arctica, C. edentula, C. lapponica*, and *C. lacustris*) evolved, with a secondary penetration of the Old World by the northern *C. arctica sensu* Pobedimova (a "pseudorelict" in the White Sea) and by *C. lapponica*, the more recent migrant. In agreement with Fernald (1922), Pobedimova considered *C. californica* and *C. edentula* as disjunct descendants of a boreal-American taxon. *Cakile lacustris* was presumed to have evolved in the Great Lakes region after a marine invasion of that area in the Quaternary. In many respects my views on the probable phylogeny of the sea rockets coincide with those of Pobedimova; differences in our taxonomies, however, necessitate a different evolutionary reconstruction for several taxa.

The tribe Brassiceae, with which *Cakile* is associated and in which it most likely evolved (see section on generic affinities), is native exclusively to the Old World, primarily to the Mediterranean region, with a single exception (Schulz 1936). Only strand plants of *Cakile* have reached and colonized the New World, undoubtedly enabled by their distinctive dispersal ecology. The inland species of *Cakile, C. arabica*, which represent the phyletic stock from which *Cakile* evolved. Morphologically, *C. arabica* is the only species in the genus possessing characteristically pubescent leaves, a feature often encountered in other genera of Brassiceae. This desert species presumably gave rise to a strand species in the Mediterranean area (the shores of the ancient Tethys Sea)

which inherited several features preadapting it to a coastal environment: an annual growth cycle, fleshy leaves, and a corky fruit capable of floating. In this new habitat *Cakile* expanded in range and speciated in regions where a degree of genetic isolation was imposed by geography, becoming the only crucifer and one of the few vascular plants growing widely on sandy beaches in the northern temperate zone.

Pobedimova (1963) proposed that *Cakile arabica* is secondarily a desert plant and was primarily a coastal species now relict following the retreat of Tethyan water from western Asia. The idea is plausible but an unnecessary complication. *Cakile arabica* does not grow on the strand of the Persian Gulf (*contra* Hultén 1945) nor on the shores of the Red Sea or Indian Ocean where it might be expected had it once been a strand plant of the eastern Tethys. Its very small fruits would appear to be poorly adapted to water dispersal. There is no compelling reason to assume that the present habitat of this species is anything other than its original one.

An age can be postulated for the strand species of *Cakile* based on distributional evidence of a negative sort. In the Old World, *Cakile* is absent from the shores of the Persian Gulf and Indian Ocean where the ancient Tethys extended into early Miocene time (Kummel 1970). If present on the strand of the Miocene Tethys Sea, sea rockets should occur today on the coasts of the Indian Ocean and Persian Gulf. In the New World, *Cakile* is absent from the Pacific Coast of Central and South America and, except where naturalized, absent also from the Pacific Coast of North America. A water passage between the Caribbean and Pacific existed, however, into the late Pliocene when the Isthmus of Panama arose (Dunbar & Waage 1969; Kummel 1970). If present in the Caribbean before late Pliocene times, *Cakile* should have been transported by the currents to the Pacific Coast, where in fact two species have become widely naturalized. From its present natural distribution, therefore, I would argue that *Cakile* is no older than early Miocene and possibly only late Pliocene in origin. The age of the Cruciferae as a family is not well established. Couper (1960) reported fossil pollen of the family from Cretaceous deposits in New Zealand, and Becker (1961) described a fruit impression of *Thlaspi primaevum* from the late Oligocene Ruby River shales of Montana. Thus the Cruciferae had apparently evolved by Miocene times and possibly much earlier.

For the Old World *Cakile euxina* (treated here as *C. maritima* ssp. *euxina*) Pobedimova (1963) concluded that it must be of late Pliocene age or even younger since the species is absent from the Caspian Sea which was long united with the Black Sea during the Pliocene (Kummel 1970). At the beginning of the Pleistocene the Black Sea and the Mediterranean were joined (Kummel 1970), and at that time *Cakile* may have first entered the Black Sea. The connection with the Mediterranean was recurrently closed and opened during the Pleistocene in response to

fluctuating sea levels associated with glaciation (Frenzel 1968; Flint 1971), and the genetic isolation imposed on the Black Sea *Cakile* during periods of separation must have been sufficient to allow the differentiation of a distinct subspecies. At the last, Weichselian glacial maximum, ca. 18,000 years B.P., the Black Sea was separated from the Mediterranean (Flint 1971) and again united by a narrow channel with the Caspian Sea (Frenzel 1968; Flint 1971). This connection was apparently not wide enough or long enough in duration to permit *Cakile* to migrate into the Caspian. Following the last glaciation, this channel was eliminated by crustal uplift, and the connection between the Black Sea and the Mediterranean was reestablished. Only recently (ca. 3000–7000 years B.P.) has the Black Sea changed from freshwater to saltwater conditions under the influence of this reunion (Degens, Watson & Remsen 1970). If pre-Weichselian in age, therefore, *C. maritima* ssp. *euxina* has experienced a change in habitat from freshwater to saltwater strand—the reverse of what must have occurred as sea rockets from the Atlantic Coast of North America colonized the shores of the freshwater Great Lakes following the Wisconsin glaciation.

Pleistocene glaciation must also have influenced the evolution of *Cakile maritima* ssp. *baltica*, growing presently on the shores of the Baltic Sea and the Skaggerak and Kattegat channels. At the last glacial maximum the Baltic Sea region was completely covered by the Scandinavian Ice Sheet, which in conjunction with the British Isles Ice Sheet also covered great portions of the North Sea (Frenzel 1968; Flint 1971). With the subsequent melting of the glacial ice, a cold lake (Baltic Ice Lake) formed ca. 10,000–12,000 years B.P., which eventually united (as the Yoldia Sea, ca. 9000 years B.P.) with the contemporaneously developing North Sea (Flint 1971). It is probable that *Cakile* entered the ancestral Baltic Sea area at this time. Crustal uplift, in the wake of the ice sheet's retreat, then isolated this body of water (the Ancylus Lake) for roughly 2000 years, ca. 7000–9000 years B.P., during which time a distinct subspecies could have diverged under genetic isolation from typical *C. maritima*. Union with the North Sea was re-established ca. 7000 years B.P. (the Littorina Sea), continuing to the present via the Skaggerak and Kattegat Channels where plants intermediate between *C. maritima* ssp. *baltica* and typical *C. maritima* now occur.

Pleistocene glaciation must also have eliminated habitats in Iceland, the Faeroes, and northern Scandinavia where *Cakile arctica* now grows. Glacial refugia in this area (Steindorsson 1963) may have provided a suitable habitat for sea rockets, but their absence from Greenland argues against the adaptation of *Cakile* to such cold conditions. The possibility of the origin of progenitors of *C. arctica* from North America by long-distance dispersal via the Gulf Stream (Löve 1963) can not be easily discounted. The Gulf Stream system may be geologically old; Schuchert (1935) stated that it developed in late Miocene-early Pliocene

time. *Cakile arctica*, however, exhibits no preponderant morphological similarities to the American taxa. Pobedimova (1963) maintained that the subarctic sea rockets were derived from North American *Cakile* because they share similar fleshy, ± entire leaves. However, plants of *C. maritima* ssp. *maritima* with fleshy, ± entire leaves occur in Western Europe and the Mediterranean region, and in floral morphology *C. arctica* is more similar to *C. maritima* than to the American *C. edentula*. *Cakile arctica* could have evolved from Western European *C. maritima* after the last glacial maximum following the chance dispersal of propagules to Iceland and differentiation there in response to insular isolation; populations in the Faeroes and northern Scandinavia could then have been established by disseminules carried by the major currents in this region. The origin of *C. arctica* must in any case have been from southern stocks, but whether American or European cannot be determined on the basis of present information.

Since I consider the sea rockets to be monophyletic and derived from Old World ancestors, their presence in the Americas raises problems of origin and dispersal. Unless one assumes an origin in the early Tertiary when North America and Europe were physically closer to one another than now (Pitman & Talwani 1972; Phillips & Forsyth 1972) long-distance dispersal must be invoked to account for the entry of *Cakile* into the New World. A chance dispersal might have occurred via the Canaries Current. Pobedimova (1963) argued that *C. fusiformis* (treated here as *C. lanceolata* ssp. *fusiformis*) was the ancestral stock of the American taxa, and she linked this taxon with *C. arabica* because of the similarly pinnatifid leaves. She also interpreted the occasional occurrence of incumbent seeds in *C. fusiformis* as indicating a relationship with *Erucaria* (which, however, commonly has conduplicate cotyledons; cf. Schulz 1936). In addition, Pobedimova described the distribution of the two species as relictual from an ancient Tethyan pattern and, citing Guppy as authority, referred to the presence of *C. fusiformis* in the Azores as an intermediate station linking their present ranges. This last idea, however, involved a misreading of Guppy (1917) who wrote of the occurrence of *C. edentula* in the Azores as a probable ballast weed. Moreover, her morphological argument is insupportable. Pinnatifid leaves are encountered sporadically in *C. lanceolata* ssp. *lanceolata*, more commonly in *C. lanceolata* ssp. *fusiformis*, and characteristically in *C. lanceolata* ssp. *pseudoconstricta* as well as in *C. maritima*. Incumbent cotyledons are found in all the taxa of *Cakile* in a small proportion of any large population sample. Since the present range of *C. lanceolata* ssp. *fusiformis* encompasses areas which were inundated during the Pleistocene, it seems plausible to regard this taxon as recent in origin; it may have arisen as a hybrid between the Antillean *C. lanceolata* ssp. *lanceolata* and the Yucatan endemic *C. lanceolata* ssp. *alacranensis*. A pivotal role for *C. lanceolata* ssp. *fusiformis* in the evolution of the American taxa

is not indicated by the morphological and distributional data. No existing taxon, in fact, provides a clear intermediate between the New World and Old World sea rockets. From considerations of the patterns of seed glucosinolate composition, however, a guess can be made concerning a probable route of entry for *Cakile* into the New World.

The seed glucosinolate compositions of *Cakile* constitute three general chemical patterns: Mediterranean, Amphi-Atlantic, and Caribbean (to use the descriptive terms suggested by Dr. Martin Ettlinger in a personal communication). The Mediterranean pattern is found in *C. maritima* ssp. *maritima* on the Pacific Coast of North America and in Australia (see section on biochemical systematics) and in the Mediterranean sea rockets (unpublished results). It is distinguished by high amounts of *sec*-butyl and isopropyl glucosinolates and a series of methylthioalkyl glucosinolates. The Amphi-Atlantic pattern, distinguished by high amounts of *sec*-butyl and/or allyl glucosinolates, is encountered in *C. edentula* ssp. *edentula* and *C. maritima* ssp. *baltica* (as previously noted) as well as in Western European sea rockets (unpublished results). The Caribbean pattern, characterized by the predominance of 3-butenylglucosinolate, is found in *C. edentula* ssp. *Harperi* and in the sea rockets of the West Indies and Gulf of Mexico. The presence of a similar glucosinolate composition in Western European and North American sea rockets is an affinity possibly arising from common descent. The progenitors of the American taxa may have originated from the coasts of Western Europe and have colonized first the Atlantic Coast of North America. The introduction, by chance long-distance dispersal, presumably involved only a single phyletic group. This founder group then colonized southward and differentiated into the several taxa now found in the West Indies and Gulf of Mexico. The change to the Caribbean pattern of seed glucosinolates apparently occurred early in the evolution of the American taxa since it characterizes *C. edentula* ssp. *Harperi* on the Atlantic Coast south of Cape Hatteras. My bias in this speculation for an original locus of introduction on the Atlantic Coast rather than in the West Indies also arises from a consideration of the annual growth cycle of *Cakile*. The European sea rockets, as with many other strand plants of that area (Chapman 1964), are annuals. Such a growth cycle is adaptive on the Atlantic Coast of North America where seasonality is pronounced. An annual growth cycle in the strand plants of the subtropical West Indies is anomalous, however, as Sauer (1967, 1972) has pointed out. The movement of *Cakile* into the West Indies may be a quite recent (?Pleistocene) event. This would explain its absence from the Pacific Coast of Central America despite the presence of a sea passage enduring until late Pliocene time.

From an original locus of colonization on the Atlantic Coast, migrations occurred southward into the islands of the Antilles and perhaps, to some degree, northward. On the coast of the Yucatan Peninsula or on the

islands formed in this area during periods of higher sea level in the Pleistocene (Wilhelm & Ewing 1972), *Cakile lanceolata* ssp. *alacranensis* became differentiated. *Cakile geniculata* evolved in the northwestern corner of the Gulf of Mexico, presumably then in relative isolation, although it is widely sympatric today with *C. constricta* in the east and *C. lanceolata* ssp. *pseudoconstricta* in the west. East of the Mississippi Delta, *C. constricta* evolved along the coast of the southeastern United States or on the northernmost islands of the Florida Platform during Pleistocene time. Since the Oligocene and particularly during the Pleistocene, the Florida Peninsula has been emergent not as a continuous landmass but as a series of low, scattered, calcareous islands, sensitive to fluctuating sea levels (MacNeil 1950; Kummel 1970). *Cakile lanceolata* ssp. *pseudoconstricta* may have differentiated on the southernmost of these islands, south of *C. constricta*. With the emergence of the Florida Peninsula after the last glaciation the range of *C. constricta* was interrupted and the gap in southern Florida was occupied by *C. lanceolata* ssp. *pseudoconstricta* and *C. lanceolata* ssp. *fusiformis*. The latter is probably a recent introduction via the Gulf Stream from the eastern shores of the Yucatan Peninsula or the Bay of Honduras. Fosberg (1963) considered it remarkable that minor but very real geographic variation occurred in widespread tropical strand species, presumably plants with great dispersibility thus promoting rapid gene exchange between populations. Geographic variation in the Gulf and West Indies sea rockets is no less real, though often minor, and it would undoubtedly be more comprehensible were more known of the shifting mosaic of land and sea in this region. The confused historical geology of the Caribbean-Gulf of Mexico region (Schuchert 1935; Woodring 1954; Graham & Jarzen 1969; Wilhelm & Ewing 1972) dampens any speculation beyond the relatively crude reconstruction attempted here.

Along the Atlantic Coast of North America, *Cakile edentula* evolved into a northern race, ssp. *edentula*, and a southern race, ssp. *Harperi*, both of which are presently sympatric on the Outer Banks of North Carolina. The transition between the two subspecies, occurring in the vicinity of Cape Hatteras, correlates with a major biogeographic and geomorphological boundary (Burk 1968; Milliman, Pilkey & Ross 1972). Ecological associates of the northern *C. edentula* ssp. *edentula*, such as the dune grass *Ammophila breviligulata* and *Hudsonia tomentosa*, also terminate their ranges on the Outer Banks. Seneca and Cooper (1971) and Seneca (1972) have shown that the transition from *Ammophila breviligulata* north of Cape Hatteras to *Uniola paniculata* southward involves a complex of interactions with temperature, water, and biotic factors in the environment. The evolution of two subspecies of *Cakile* north and south of Cape Hatteras may have similarly involved adjustments to some of these differing climatic and biotic conditions. While no obvious geographic barrier separates the two today, the environments of

these subspecies are strongly influenced by two very different current systems of the North Atlantic Ocean, the warm Gulf Stream south of Cape Hatteras and the cold Labrador Current north of it (Cotter 1965). In the Hatteras offshore waters where they meet, they create a barrier to migration as effective as any landmass separating two bodies of water. Despite the clear potential for gene flow through hybridization, the integrity of each seems little affected by the other. Strong environmental selection or an absence of significant dispersal due to the opposing current systems, or both, may operate in maintaining the identity of these two subspecies.

The range of *Cakile edentula* ssp. *edentula* must have been severely restricted by the Laurentide Ice Sheet about 20,000 years B.P. when it completely covered the Great Lakes Basin, the valley of the St. Lawrence River and the Gulf of the St. Lawrence, and the eastern coast of North America south to Long Island (Flint 1971). With the melting of the glaciers, coastal habitats were reopened to northward colonization by *C. edentula*. Moreover, the Great Lakes were formed after the last glacial maximum, about 15,000 years B.P. (Hough 1963). *Cakile* and other plants may have entered the Great Lakes region nearly this early by long-distance dispersal overland from the Atlantic Coast. More plausibly, however, *Cakile* could have colonized the region about 11,500–9,500 years B.P. when a marine embayment known as the Champlain Sea extended from the Gulf of St. Lawrence to, or nearly to, old Lake Ontario (Hough 1958, 1963; Elson 1969; Dorr & Eschman 1970). This embayment would have provided a continuous route for the migration of strand species from the Atlantic Coast into the Great Lakes Basin. Isostatic uplift in the St. Lawrence River valley forced the retreat of these marine waters (Hough 1963), which could then have isolated the Great Lakes *Cakile* from its maritime congener. This geographic isolation may then have enforced the differentiation of a new taxon, *C. edentula* ssp. *edentula* var. *lacustris*. Seneca and Cooper (1971) demonstrated ecotypic differences in *Ammophila breviligulata* from the Great Lakes strand and the Atlantic Coast of North Carolina. Adaptation to the freshwater littoral has probably occurred in *C. edentula* var. *lacustris* as well although the differences in fruit and seed morphology distinguishing it from *C. edentula* var. *edentula* do not appear to be of adaptive significance. Based on a limited study, Chrysler (1904) reported that the Great Lakes *Cakile* has less succulent leaves than Atlantic Coast *C. edentula*, a phenomenon often encountered in plants which shift from a saltwater to freshwater strand habitat (Boyce 1954). The affinities between several Atlantic Coast and Great Lakes plants were early pointed out by John Torrey (1843). Knowing of the occurrence of marine clay deposits near Lake Ontario, he hypothesized that the disjunctions arose following the migration of these plants after the melting of the ice sheet when the Great Lakes were a marine body of water united to the Atlantic

Ocean via the St. Lawrence. Drummond (1867) and Hitchcock (1871) also supported this interpretation. Increased knowledge of the geology of the Great Lakes negated this view of an extensive marine stage, however. As the concept of the Champlain Sea embayment gained acceptance, Marie-Victorin (1916) and Svenson (1927) proposed that many of the disjuncts used this as a migratory route. This route is the most plausible one for those plants primarily dispersed over many miles by water. It may not have served as such for all the strand disjuncts between the Great Lakes and the Atlantic Coast (e.g., *Ammophila breviligulata, Euphorbia polygonifolia, Hudsonia tomentosa*), nor was it likely the only means of entry for the larger number of Atlantic Coastal Plain species disjunct in the Great Lakes basin (Peattie 1922), many of which could have been dispersed overland.

Pleistocene conditions, particularly the general cooling induced by the glaciation, may also have influenced events in Bermuda. As noted in the section on biochemical systematics, my analyses of two Bermuda samples revealed a distinctive seed glucosinolate composition of the Amphi-Atlantic pattern. This pattern is characteristic of northern taxa of *Cakile* such as *C. edentula* ssp. *edentula, C. arctica,* and *C. maritima* ssp. *baltica.* Morphologically, these Bermuda plants had fleshier leaves and smaller fruits than is typical of *C. lanceolata* with which most of the Bermuda herbarium collections agree. It is possible that a distinct race evolved in Bermuda during cooler Pleistocene times and that this race possessed a characteristically northern glucosinolate composition, either because the populations were founded by migrants which possessed an Amphi-Atlantic pattern or because there was selection for this character under the cool conditions then prevailing. Recurrent introductions of *C. lanceolata* via the Gulf Stream, perhaps accelerating with post-Pleistocene warming, suppressed any further evolution and created the heterogeneity in Bermuda material observed by Pobedimova (1963, 1964) and others.

With some hesitation, Figure 11 is presented to summarize the phylogeny of *Cakile*. Any scheme such as this grossly oversimplifies the arguments behind it which in the absence of a fossil record, must oversimplify a dynamic process. Throughout, an attempt has been made to find a plausible background for geographic isolation to account for the observed differentiation in *Cakile*. Isolated bodies of water obviously provide a locus for speciation, but island settings, too, may lead to fragmented populations and reduced gene flow and thereby promote evolution. Insular evolution undoubtedly accounts for the origin of *C. arctica* and may well have generated most of the patterns of geographic variation in the Caribbean and Gulf of Mexico. Little more than speculation can be offered regarding the selective value, if any, of the characters distinguishing the taxa. Increased fruit length in *C. arctica* and *C. lanceolata* ssp. *lanceolata* may, for example, confer greater buoyancy and improve

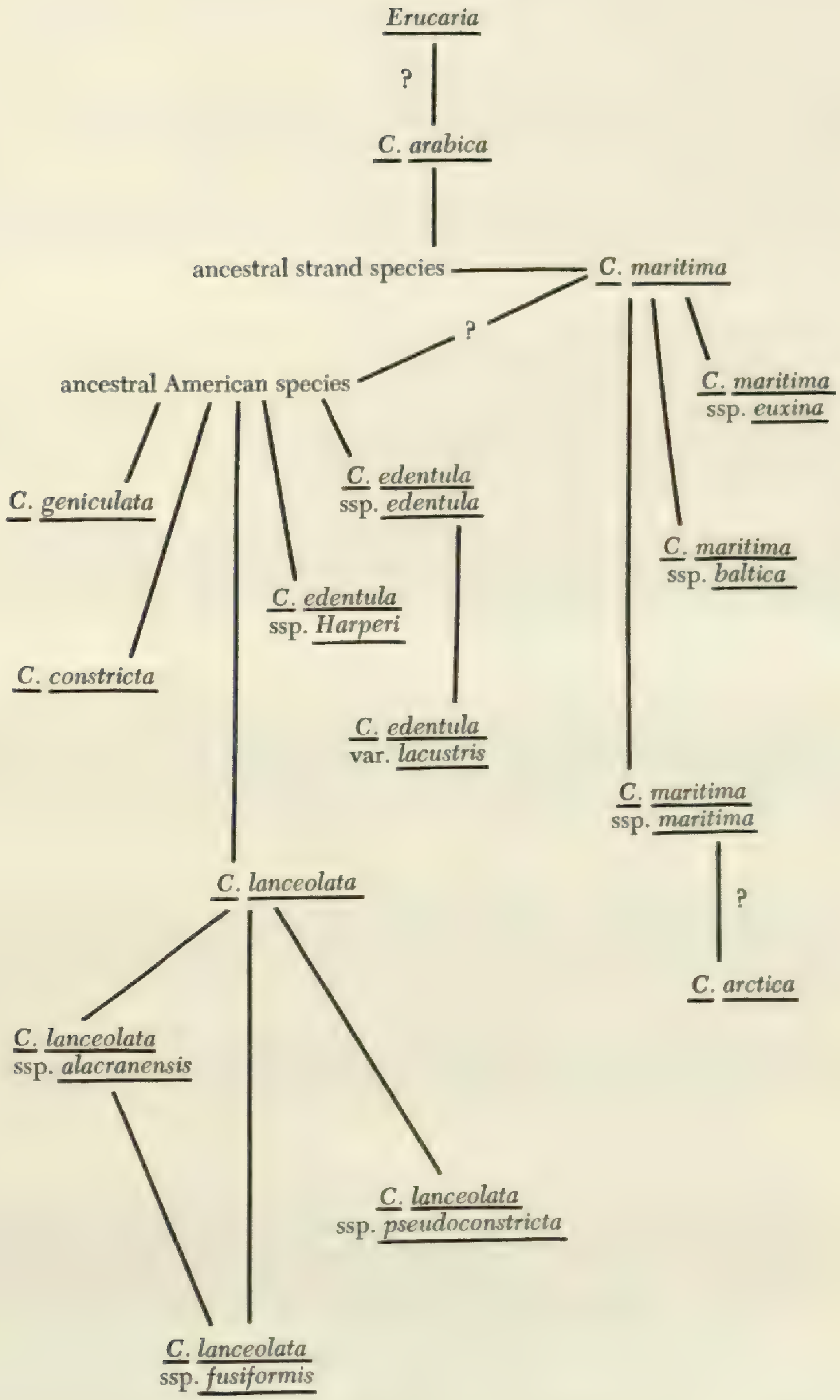


Figure 11. Proposed phylogeny of the genus *Cakile*. Read from top.

dispersibility. Small flowers may be part of a syndrome for autogamy promoting high fruit set in seasonally restricted habitats. In some cases the differentiated features may be without adaptive value but result instead from random genetic drift. Ultimately, ecological work like that of Barbour (1972) and my own experiments on fruit flotation and seed viability may contribute to an understanding of natural selection in the evolution of *Cakile*.

Economic Use

"There is no Beauty or Use in these Plants at present known, but they are preserved in Botanic Gardens for Variety."

(Philip Miller, 1748)

Notwithstanding the noted English gardener's comment, sea rockets have been utilized by man in a number of ways through the ages. Markgraf (1963) reported that in the Old World *Cakile* was employed as an antiscorbutic, diuretic, and purgative in folk remedies. The leaves were eaten in salads, and plants were even cultivated on a small scale in France for this purpose (Pobedimova 1963). In the New World, Linnaeus' student Peter Kalm observed that in time of famine the Indians along the St. Lawrence River pounded the roots of "*Bunias cakile*" into powder which, mixed with other flours, was made into bread (Benson 1966). The colonial Europeans also learned to exploit the plants. As in the Old World, sea rockets were eaten for their antiscorbutic properties; and Small (1900) stated: "[T]he scurvy dispelling properties of this plant *[Cakile lanceolata]* have been tested and found effective." From De la Sagra's account (1853) one may surmise that sailors in the West Indies were not especially opposed to the remedy for scurvy since it usually consisted of "la raiz en infusion en vino blanco." Leaves of sea rockets were likewise eaten in salads (Questel 1951; Marie-Victorin & Rolland-Germain 1969). On personal examination I found the young leaves to have a pleasant, mildly biting flavor, reminiscent of horseradish. The flavor is caused in part at least by the plant's mustard oils. Fernald, Kinsey, and Rollins (1958) report an observation made by Harold St. John that Labrador fishermen often gather large quantities of the young plants of *C. edentula* to cook as a potherb. In the Bahamas, sea rockets are occasionally gathered as forage for the local burros, hogs, and goats (Howard 1950). A specimen of *C. edentula* collected in Grays Harbor County, Washington (*Foster 1534*, US), bears the charming comment on its label: "Cattle are very fond of it."

Undoubtedly the chief benefits which man derives from these plants are the indirect ones arising from their ecological role as pioneers in beach and dune successions. This aspect of the biology of *Cakile* is treated more fully in the section on habitat and range.

TAXONOMIC TREATMENT

Cakile Miller, The Gardeners Dictionary . . . Abridged, 4th Edition, Vol. 1. 1754.

Plants annual or fortuitously perennial, herbaceous to occasionally suffrutescent, fleshy, glabrous to rarely pubescent, much-branched near the base, the branches spreading and ascending, curved to flexuous, or prostrate, decumbent to procumbent, with a stout woody taproot and long thin horizontal roots. First leaves large (to 15 cm), later ones progressively smaller, broadly ovate and petiolate to obovate, spatulate, or oblanceolate or deeply and finely pinnatifid, margin sinuate or crenate to variously lobed, the lobes usually rounded and irregularly spaced; hydathodes often at the tips of leaves. Flowers borne in terminal elongating racemes, the lowest flower occasionally subtended by a leaf-like bract; pedicels ca. 1–10 mm long, < 1–3 mm wide, divergent, rarely ascending or recurved in fruit; sepals 4, green, erect at anthesis, deciduous, ovate, 3–5 mm long, 1.5–3 mm wide, margins hyaline, subcucullate at apex, slightly dimorphic, the laterals somewhat gibbous at the base and usually more acute at the apex; the outer upper surface often with sparse simple trichomes, petals 4 (rarely absent or present only as bristles), obovate or spatulate to distinctly unguiculate, the blade reflexed in flower, entire, sinuate, or emarginate, white, pinkish purple, or lavender; nectar glands 4, green, dimorphic, the laterals bilobed, appressed to the base of the pistil, the lobes ± orbicular, the medians conical to tetrahedral or when small ± orbicular; stamens tetradynamous but becoming less so as flower ages, the filaments stout, tapering abruptly at apex, the anthers bilocular, rounded to apiculate at apex, saggitate at base, the laterals dehiscing introrsely within the flower, the medians dehiscing introsely to latrorsely level with the petal blades to slightly exserted; pistil sessile, ovate to ensiform, style lacking, the stigma hemispherical or occasionally bilobed, capitate to retuse at apex of stylar beak. Immature fruit fleshy, green, becoming dry and corky, of 2 indehiscent segments, both falsely 1-loculed and usually 1-seeded (occasionally aborted or 2- 3-seeded), the septum a white papery-thin membrane appressed longitudinally to each seed, the upper beaked segment deciduous by a transverse articulation often incomplete in its center; lower proximal segment terete to vaguely angled or ribbed, with or without prominent lateral, usually reflexed horns, the articulating surface often with 2(6) small, ascending, conical teeth; upper distal segment terete to angled, ribbed, or furrowed, the beak acute to retuse, conical to flattened in one plane, the base occasionally with a scarious margin, the articulating surface with pits corresponding to the teeth on the lower segment. Seeds accumbent to occasionally obliquely incumbent, ellipsoid to narrowly oblong, flattened longitudinally, puncticulate to smooth, variously brown or bronze, dimorphic, the upper erect seed larger than the lower pendulous seed. Fruiting racemes linear to distinctly geniculate. Cotyledons fleshy, ± equal, lanceolate or oblanceolate. Pollen grains yellow, tricolpate, reticulate, spherical to oblate-spheroidal when turgid. CHROMOSOME NUMBER $2n=18$. Lectotype species: *Cakile maritima* Scop.

KEY TO THE SPECIES

A. Leaves deeply and finely pinnatifid, usually pubescent; fruits < 4 mm wide, the articulating surface of the lower segment with 2 stout vertical, conical teeth 1–2 mm high. . . . . 5. *C. arabica*.

A. Leaves entire to deeply pinnatifid, never pubescent; fruits > 3 mm wide, the articulating surface of the lower segment flat or with teeth 1 mm high or less. B.

B. Fruiting pedicels 5–10 mm long; fruits constricted at the articulation, > 20 mm long when both segments fertile; petals usually > 3 mm wide. 6. *C. arctica*.

B. Fruiting pedicels usually < 5 mm long; fruits constricted or not at articulation, 13–31 mm long; petals 1.5–6 mm wide. C.

C. Lower fruit segment with 2 opposite lateral horns or the sides prolonged upward into 2 sharp triangular wedges, concave between; petals 3–6 mm wide, lavender to less commonly white. . . . . 1. *C. maritima*.

C. Lower fruit segment without lateral horns and if prolonged upward, the wedges < 1.5 mm high; petals < 4.5 mm wide, often < 3 mm, white to lavender. . . . . D.
D. Infructescence usually > 2 dm long; leaves not particularly fleshy; plants usually sprawling; petals usually > 3 mm wide and white. . . . . 2. *C. lanceolata.*
D. Infructescence usually 1–2 dm long; leaves fleshy; plants erect to compactly prostrate; petals usually < 3 mm wide, lavender to white. . . . . E.
E. Infructescence geniculate, the pedicel as broad as the rachis in fruit; petals < 2 mm wide. . . . . 4. *C. geniculata.*
E. Infructescence linear or sinuous, the pedicels not as broad as the rachis in fruit; petals 1.5–3 mm wide. . . . . F.
F. Fruit 8-ribbed, or 4-angled and short-beaked, 5–9 mm wide, or slender and long-beaked, the beak somewhat flattened in one plane and retuse or blunt at the apex, rarely acute. . . . . 3. *C. edentula.*
F. Fruit terete to 4-angled, 3–4 mm wide, the beak conical and acute at the apex. . . . . 7. *C. constricta.*

1. Cakile maritima Scopoli

Fleshy, herbaceous to occasionally suffrutescent annuals or fortuitous perennials, erect to prostrate, occasionally forming dense mounds up to 8 dm high and 12 dm across, much-branched, the branches ascending or lax; first leaves large, up to 10 cm long, petiolate, ovate or lanceolate to deeply pinnatifid with 6–9 lobes, often with a grayish green hue, later leaves smaller, often entire; racemes elongating in fruit to 2–4 dm long, linear, never geniculate; pedicels divergent to rarely reflexed, 1–3 mm wide, 1.5–7 mm long; sepals ovate, 4–5.5 mm long, bigibbous, occasionally with sparse simple trichomes near the apex; petals usually distinctly clawed, 8–14 mm long, 3–6 mm wide, pale purple or rose-purple to rarely white; nectaries large, the medians 0.4–0.7 mm high; stamens tetradynamous, the anthers 1.4–2.2 mm long, dehiscing introrsely to latrorsely; pistil lanceolate; stigma capitate; mature fruit 12–27 mm long, 4–8 mm wide, ± hastate and with two reflexed lateral horns on the lower segment or deltoid; the lower fruit segment ± conical, expanding toward the apex, often with two opposite lateral horns projecting just below the articulating surface, this surface broad and flat, concave, or convex; the upper fruit segment mitriform or conical, terete or tetragonal, acute to blunt at the apex, with a scarious basal margin; seeds ellipsoid and dimorphic; cotyledons accumbent to occasionally incumbent or contorted.

KEY TO THE SUBSPECIES

A. Leaves entire to pinnatipartite, the lobes obovate or spatulate, rarely sinuately lobed themselves, and rarely less than 5 mm wide. . . . . 1a. *C. maritima* ssp. *maritima.*
A. Leaves deeply pinnatifid, often 2-pinnatipartite, the lobes linear and 1–5 mm wide. . . . . B.
B. Fruits ± hastate and constricted at the point of articulation. . . . . 1b. *C. maritima* ssp. *baltica.*
B. Fruits deltoid in outline, not constricted at the point of articulation. . . . . 1c. *C. maritima* ssp. *euxina.*

1a. Cakile maritima Scop. ssp. maritima

PLATE 1; MAP 1.

Cakile maritima Scop., Fl. Carn. ed. 2, **2**: 35. 1772; based on *Bunias Cakile* L., Sp. Pl. 2:670. 1753. Lectotype: Portugal, "S. Ybes [Setubal] in littore marini," *Loefling s.n.* (LINN 847.6, not seen; photo: A).

Rapistrum cakile (L.) Crantz, Class. Crucif. 106. 1769.

Bunias littoralis Salisb., Prodr. 273. 1796. An avowed new name for *B. Cakile* L.

Cakile Cakile (L.) Karsten, Deutsche Fl. Pharm.-med. Bot. 663. 1882.

Crucifera cakile (L.) Krause in Sturm, Fl. Deutsch. ed. 2, 138. 1902.

Rapistrum maritimum (Scop.) Berger., Phytonomat. 173. 1784.

Cakile maritima var. *latifolia* Desf., Fl. Atl. 2: 77. 1798. Holotype: without data (P, seen on microfiche: IDC 6210. 38: II. 2.).

Cakile latifolia (Desf.) Poir., Ency. Bot. Suppl. 2: 88. 1811.

Cakile aegyptia var. *latifolia* (Desf.) Maire, Fl. Afr. Nord. 12: 402. 1965.

Cakile maritima var. *integrifolia* Boiss. non Koch. Fl. Or. 1: 365. 1867. Syntypes: Egypt, Alexandria, *Samar s.n.*, and Turkey, Moeotidum. *Stev s.n.* (?G; not seen).

Cakile maritima var. *laciniata* Hallier. Fl. Deutsch. 15: 44. 1883. Type: Germany, Helgoland (?JE; not seen).

Cakile maritima var. *pandataria* Terraciano, Ann. Acad. Aspir. Nat. Ser. 3, 1: 5. 1884. Type: Italy, Naples (?NAP; not seen).

Cakile maritima f. *pandataria* (Terrac.) O. E. Schulz in Urb., Symb. Antill. 3: 504. 1903.

Cakile maritima var. *auriculata* Post. Fl. Syr. Pal. Sin. 103. 1896. Type: not known.

Cakile maritima var. *amblycarpa* O. E. Schulz in Urb., Symb. Antill. 3: 503. 1903. Type: none specified.

Cakile maritima var. *oxycarpa* O. E. Schulz in Urb., Symb. Antill. 3: 503. 1903. Type: none specified.

Cakile maritima var. *sessiliflora* O. E. Schulz in Urb., Symb. Antill. 3: 504. 1903. Type: none specified.

Cakile maritima f. *pygmaea* O. E. Schulz in Urb., Symb. Antill. 3: 504. 1903. Type: none specified.

Cakile maritima var. *susica* Maire, Weiller & Wilczek, Bull. Soc. Hist. Nat. Afr. Nord 26: 120. 1935. Type: Morocco, "in arenis ad ostium fluminis Sous," *Maire et al. s.n.* (?).

Cakile aegyptia var. *susica* (Maire, Weiller & Wilczek) Maire, Fl. Afr. Nord 12: 402. 1965.

Isatis aegyptica L., Sp. Pl. 2: 671. 1753. Type: not known; not in LINN (cf. Savage 1945).

Cakile aegyptiaca (L.) Willd., Sp. Pl. 3: 417. 1800.

Cakile maritima var. *aegyptiaca* (L.) Delile, Fl. Aegypt. 19. 1813.

Cakile maritima var. *integrifolia* Koch non Boiss., Syn. Fl. Germ. 77. 1835. An avowed new name for the preceding.

Cakile maritima ssp. *aegyptiaca* (L.) Nyman, Consp. 29. 1878.

Isatis pinnata Forsk., Fl. Aegypt. 121. 1775. Lectotype: "ex Aegypto inser.", *Forskal s.n.* (C, seen on microfiche: IDC 2200. 58. I. 1,2.).

Cakile maritima var. *pinnatifida* Delile. Fl. Aegypt. 18. 1813. An avowed new name for the preceding.

Cakile Serapionis Gaertner. Fruct. Sem. Pl. 2: 287. t. 141. 1791. Type: not seen (?TUB).

Cakile pinnatifida Stokes, Bot. Mat. Med. 3: 484. 1812. Type: not seen.

Cakile sinuatifolia Stokes, Bot. Mat. Med. 3: 485. 1812. Type: "the shore of the Adriatic," *Agerius s.n.* (?).

Cakile maritima var. *sinuatifolia* (Stokes) DC., Reg. Veg. Syst. Nat. 2: 429. 1821.

Bunias ovalis Viv., Fl. Lib. 35. t. 16, fig. 3. 1824. Type: Libya, "in littore Pentapoleos" (?GE; not seen).

Cakile cyrenaica Sprengel, Syst. Veg. 2: 852. 1825. An avowed new name for the preceding.

Cakile crenata Jordan. Diagn. 1: 346. 1864. Type: none specified.

Cakile edentula Jordan non (Bigel.) Hook., Diagn. 1: 344. 1864. Type: none specified.

Cakile maritima var. *edentula* (Jord.) Loret in Loret & Barr., Fl. Montp. ed. 2. 50. 1888.

Cakile maritima "proles" *edentula* (Jord.) O. E. Schulz in Urb., Symb. Antill. 3: 503. 1903.

Cakile aegyptia var. *edentula* (Jord.) Maire, Fl. Afr. Nord 12: 402. 1965.

Cakile hispanica Jordan, Diagn. 1: 345. 1864. Type: none specified.

Cakile maritima var. *hispanica* (Jord.) Paol. in Fiori & Paol., Fl., Anal. Ital. 1: 453. 1898.

Cakile aegyptia var. *hispanica* (Jord.) Maire, Fl. Afr. Nord 12: 403. 1965.
Cakile littoralis Jordan, Diagn. 1: 345. 1864. Type: none specified.
Cakile maritima var. *australis* Cosson in Loret & Barr., Fl. Montp. 1: 64. 1876. An avowed new name for the preceding.
Cakile aegyptia var. *australis* (Coss.) Maire, Fl. Afr. Nord 12: 402. 1965.
Cakile maritima var. *pennatifida* Paol. in Fiori & Paol. Fl. Anal. Ital. 1: 452. 1898. An avowed new name for *C. littoralis* Jord.
Cakile maritima "proles" *litoralis* (Jord.) O. E. Schulz in Urb., Symb. Antill. 3: 503. 1903.
Cakile monosperma Lange, Descr. Icon. Ill. 1: 5. t. 7. 1864. Type: Spain, Coruna, IX–1852 (?c; not seen).
Cakile maritima var. *monosperma* (Lange) O. E. Schulz in Urb., Symb. Antill. 3: 503. 1903.

Leaves succulent, deeply pinnatifid, the lobes and rachis usually more than 5 mm wide, the lobes obovate or spatulate, 5–15 mm long, 4–8 in number, usually rounded at the apex, rarely themselves lobed, to broadly ovate or lanceolate and sinuately to dentately lobed; pedicels in fruit divergent to occasionally reflexed, 1.5–7 mm long, 1.5–3 mm wide; mature fruit 14–27 mm long, usually hastate with two opposite lateral horns on the upper part of the lower segment; the lower fruit segment conical, expanding toward apex, with two lateral horns projecting below the articulating surface, often reflexed, <1–3 mm long; upper fruit segment mitriform or conical, usually 4-angled, apex acute to blunt and usually compressed, the base with a scarious margin; when aborted, the lower segment often becomes a small knobby extension of the pedicel and the upper fruit segment is fusiform. CHROMOSOME NUMBER: $2n=18$.

DISTRIBUTION: shores of the Mediterranean Sea and of the Atlantic Ocean from Morocco to the British Isles and the North Sea to central Norway; naturalized along the Pacific Coast of North America and the temperate coast of Australia; more widely introduced as a ballast weed. Flowering probably throughout the year in southern parts of its range, but more seasonally further north.

REPRESENTATIVE SPECIMENS (native range). **Algeria:** Hussein Dey, 4–IX–1866, *Gautier 220* (DS). **Belgium:** Oostduinkerke, 26–VI–1928, *Robyns s.n.* (DAO). **Egypt:** Alexandria, 15–III–1926, *Jepson 10912* (UC). **England:** Cornwall, Port Luney, 24–VIII–1929, *Thurston 2920* (MO,US); Kent, Sandwich Bay, 11–X–1960, *Raven 15852* (RSA). **France:** Aude, La Nouvelle, 1902, *Sennen s.n.* (DS,GH); Marseille, 1821, *Solier s.n.* (NY); Corsica, Bonifacio, 1880, *Reverchon 286* (DS,NY); Landes, Mimizan Plages, 11–IX–1930, *Tidestrom s.n.* (US); Normandie, Fermanville, 24–VII–1936, *Tidestrom 14303* (MICH,NY,POM,SMU). **Germany:** Insel Baltrum, VIII–1900, *Buchenau s.n.* (GH). **Greece:** Piraeus, V–1967, *Huber s.n.* (UC); Crete, La Canee, 26–III–1914, *Gandoger 4172* (MO). **Ireland:** Co. Wexford, Rosslare, 13–VIII–1939, *O'Leary s.n.* (SMU). **Italy:** Albissola, 9–X–1882, *Piccone 3631* (DS,UC); near Naples, III–1858, *Engelmann 3622* (MO); Sardinia, Tempio, 10–VII–1881, *Reverchon 32* (DS); Sicily, Palermo, *Todaro 1351* (DS). **Lebanon:** Beirut, 14–V–1968, *Stutz 3586* (NY). **Libya:** Tobruk, 7–IV–1883, *Schweinfurth 10* (US). **Morocco:** Tangier, 18–IX–1920, *Young s.n.* (CU). **Netherlands:** Terschelling Island, 15–VIII–1951, *van Heerdt & Nijenhuis 128* (DAO, MO,NCU,NSW,SMU,WIS). **Portugal:** Porto, 1891, *Buchtien s.n.* (US). **Scotland:** Luce Bay, Wigtownshire, *Henderson 1538* (DAO,NCU). **Spain:** Alpujarras, *Wielkomm 391* (MEL,MO); Majorca, 13–IX–1907, *Knoche 2285* (DS); Cangas, near Vigo, VIII–1926, *Exell 26* (BM). **Tunisia:** Gabes, III–1907, *Pitard 37* (MEL,MO,NSW,NY). **Yugoslavia:** Brioni, 25–VI–1905, *Knoche s.n.* (DS).

REPRESENTATIVE SPECIMENS (naturalized or introduced). **Argentina:** Buenos Aires, Villa Gesell, 3–III–1961, *Burkart 22368* (UC); San Clemente del Tuyu, Partido de Lavalle, dunas, 29–I–1939, *Cabrera 4919* (GH,NY); S. Clemente del Tuyu-Medanos, 10–II–1961, *Fabris-Cullen 2532* (RSA). **Australia. South Australia:** near Beachport, ca. 80 km N.W. of Mount Gambier, 12–XI–1959, *Jackson 188* (AD); Kangaroo Island, Hog Bay, 9–II–1946, *Cleland s.n.* (AD); Kybybolite, XI–1918, *Andrew s.n.* (AD); south of Port Lincoln, 5–XI–1964, *Barbour 256* (DUKE); Pt. Noarlunga near Adelaide, XI–1943,

Perry s.n. (CANB). **Victoria:** Altona at the mouth of Skeleton Creek, 21–XI–1967, *Cullimore 104* (MEL,NSW); Beaumaris, X–1922; *Tagdell s.n.* (MEL); Phillip Island, Cowes, III–1950, *Dunk s.n.* (MEL); Shelly Beach near Portland, X–1944, *Beauglehole s.n.* (MEL); Warrnambool, 5–I–1960, *Howard s.n.* (AD). **Western Australia:** Esperance, 17–X–1968, *Eichler 20300* (AD,GH); Fremantle, 19–XII–1897, *Helms s.n.* (PERTH); Geographe Bay, E. of Busselton, 23–III–1898, *Morrison s.n.* (K); Guilderton, mouth of Moore River, 21–II–1963, *Sauer 3438* (UC); King George's Sound, VIII–1901, *Goadby 279* (DAO,NSW). **Canada. British Columbia:** Vancouver Island, near Ucluelet, 1–IX–1951, *Newton 13* (DAO,UBC). **Mexico. Baja California:** Cedros Island, 20–IV–1963, *Moran 10765* (DS,GH,RSA,SD,UC,US); San Martin Island, Hassler Cove, 10–IV–1963, *Moran 10530* (SD). **New Caledonia.** Plage de l'Anse Vata pres Noumea, 6–VIII–1950, *Baumann 5161* (US). **Uruguay.** Dep. Maldonado: Punta del Este, 3–I–1941, *Descole 65* (GH); Dep. Rocha: La Paloma, 7–XI–1934, *Herter 1704* (NY); Maravillas, 16–XI–1948, *Herter 1704a* (MO). **U.S.A. Alabama: Mobile Co.,** ballast ground of M & O R.R. wharf, 16–VIII–1891, *Mohr 21* (US). **California: Alameda Co.,** Bay Farm, 4–IX–1936, *Covel 584* (CAS); **Contra Costa Co.,** Pt. Orient, 19–VII–1958, *Robbins 3905* (UC); **Del Norte Co.,** Pt. St. George, 20–VII–1947, *Tracy 17872* (UC); **Humboldt Co.,** near Samoa, 21–IX–1940, *Tracy 16724* (DAO,DS,GH,MO,NY,UC); **Los Angeles Co.,** near El Segundo, growing across from the Hyperion Sewage Disposal Plant, IV–1961, *Bennett s.n.* (RSA); **Marin Co.,** Stinson Beach, 19–V–1935, *Rose 35178* (CAS,DS,F,MICH,MO,NY,POM,RSA,UC,US); **Mendocino Co.,** beach at creek mouth 4 miles S. of Fort Bragg, 11–VII–1941, *Heller s.n.* (DS); **Monterey Co.,** sea beach at Monterey VII–1940, *Hesse 134* (UC); **San Diego Co.,** Imperial Beach, 26–IV–1954, *Harbison s.n.* (UC); **San Francisco Co.,** near Daly City, 29–V–1949, *Weatherby 504* (RSA); **San Luis Obispo Co.,** along beach between Pismo and Oceano, VIII–1941, *Reed s.n.* (CAS); **San Mateo Co.,** Half Moon Bay, 12–II–1941, *Hoover 4753* (UC); **Santa Barbara Co.,** beach southeast of Ellwood, 15–X–1957, *Pollard s.n.* (CAS); **Santa Cruz Co.,** Aptos, 29–VII–1943, *Hesse 344* (UC); **Sonoma Co.,** near mouth of Salmon Creek, 18–VIII–1937, *Ferris 9370* (CAS,DS,GH,MICH,NY,POM); **Ventura Co.,** Ventura, 1–VIII–1958, *Pollard s.n.* (TEX). **New Jersey:** Ballast near Communipaw Ferry, IX–1880, *Brown s.n.* (F,NY). **New York: Bronx Co.,** at Longefellow and Viele Ave., 28–IX–1948, *Ahles 897* (NY). **North Carolina:** Wilmington ballast grounds, 14–VIII–1885, *McCarthy s.n.* (F,US). **Oregon: Clatsop Co.,** Garibaldi, 30–VI–1947, *Peck 24194* (CAS); **Coos Co.,** Sunset Bay, 3–VIII–1942, *Doty 5081* (DS); **Curry Co.,** strand at Humbug Mt. State Park, 10–VIII–1969, *Rodman 84* (GH); **Lane Co.,** Glenada Beach near Florence, 15–VII–1965, *Clark s.n.* (DS); **Lincoln Co.,** Newport, 25–VII–1963, *Stuckey 1929* (OS); **Tillamook Co.,** Netarts Bay, 13–VIII–1969, *Rodman 87* (GH). **Pennsylvania:** Philadelphia, Greenwich Point ballast, 26–VIII–1877, *Parker 10990* (MICH,MO,NY). **Texas:** Balls Harbor, *Reverchon s.n.* (MO). **Virginia:** Newport News ballast, 30–V–1921, *Leonard & Killip 61* (CAS,F,GA,MO,US). **Washington: Clallam Co.,** Mukkaw Bay, 22–VII–1940, *Ownbey 2260* (DS,GH,UC); **Grays Harbor Co.,** south of Westport, 12–VII–1952, *Bartlett & Grayson 643* (MICH).

Scopoli (1772) published *Cakile maritima* as a new name for Linnaeus' *Bunias Cakile* to avoid coining a tautonym. Therefore the type of *C. maritima* ssp. *maritima* is the same as the type of *B. Cakile*. However, Linnaeus (1753) founded the species on several specimens as is evident from his comment: "Habitat in Europae, Africae, Americae maritimus." A lectotype must therefore be chosen, but Pobedimova (1964) and Ball (1964a) neglected to do this. I am here designating as lectotype a sheet in the Linnean Herbarium annotated: "Bunias Kakile . . . S. Ybes," a collection from Steubal, Portugal, made by Loefling in 1751 (Ball 1964a). The specimen has pinnatifid leaves and hastate fruits with both segments apparently fertile, thus resembling most Mediterranean collections and, hence, also corresponding to Scopoli's concept of the species.

Pobedimova (1963, 1964) separated the Western European plants (as *Cakile monosperma*) from Mediterranean plants (as *C. maritima*) on the basis of the frequently aborted lower fruit segments exhibited by Western European sea rockets. This distinction was apparent in the material (ca. 300 collections) available to me for study (see section on morphology and anatomy) and must also have been evident to Schulz (1903) who made the combination *C. maritima* var. *monosperma* and commented that these plants occurred "ab ins. Helgoland ad Lusitaniam." Ball (1964a,b), however, discounted this character as too variable but proceeded to recognize a Western European subspecies (*C. maritima* ssp. *maritima*) distinct from a Mediterranean subspecies (*C. maritima* ssp. *aegyptiaca*) on the basis primarily of the flat or concave nature, respectively, of the articulating surface of the lower fruit segment. I have found this character to vary over a wide range of material although the trend is there. Ball (1964a) also had to concede that: "Plants which are almost identical with subsp. *maritima* occur sporadically throughout the range of the subspecies [ssp. *aegyptiaca*]." I prefer to make no taxonomic distinction between Western European and Mediterranean sea rockets on the basis of the characters currently investigated. While trends can be perceived (e.g., toward aborted lower fruit segments and lower segments with a flat articulating surface in Western European plants), the discontinuities are not substantial enough to warrant formal nomenclatural recognition, at least at the species or subspecies rank.

The plethora of infraspecific names for *Cakile maritima* ssp. *maritima* attests to the variation in leaf morphology, largely in the degree of lobing, variation in fruit shape, and the degree of development of the lateral horns present in these plants. However, most of this variation is apparent within individual populations and even, occasionally, on individual plants, as a critical reading of Schulz (1903, 1923) reveals. Pobedimova (1964) remarked that she could find no correlations between this variation and geographical range and consequently chose to recognize no varieties or forms, a position which I think is fully justified.

1b. **Cakile maritima** Scop. ssp. **baltica** (Rouy & Foucaud) P. W. Ball

PLATE 1; MAP 1.

Cakile maritima ssp. *baltica* (Rouy & Foucaud) Hylander ex P. W. Ball, Rep. Spec. Nov. 69: 37. 1964.

Cakile maritima f. *baltica* Rouy & Fouc., Fl. Fr. 2: 69. 1895. Syntypes: "F. Schultz Herb. norm., nov. ser., n° 1318; Reichb. n° 361.—Non encore observe en France" (?P; not seen).

Cakile maritima ssp. *baltica* (Rouy & Fouc.) Hyl., Forteck. Nord. Vaxter 64. 1955. No citation of basionym, hence illegitimate.

Cakile baltica Jordan, Diagn. 1:345. 1864. *Nomen nudum.*

Cakile maritima var. *baltica* (Jord.) Paol. in Fiori & Paol., Fl. Anal. Ital. 1: 452. 1898.

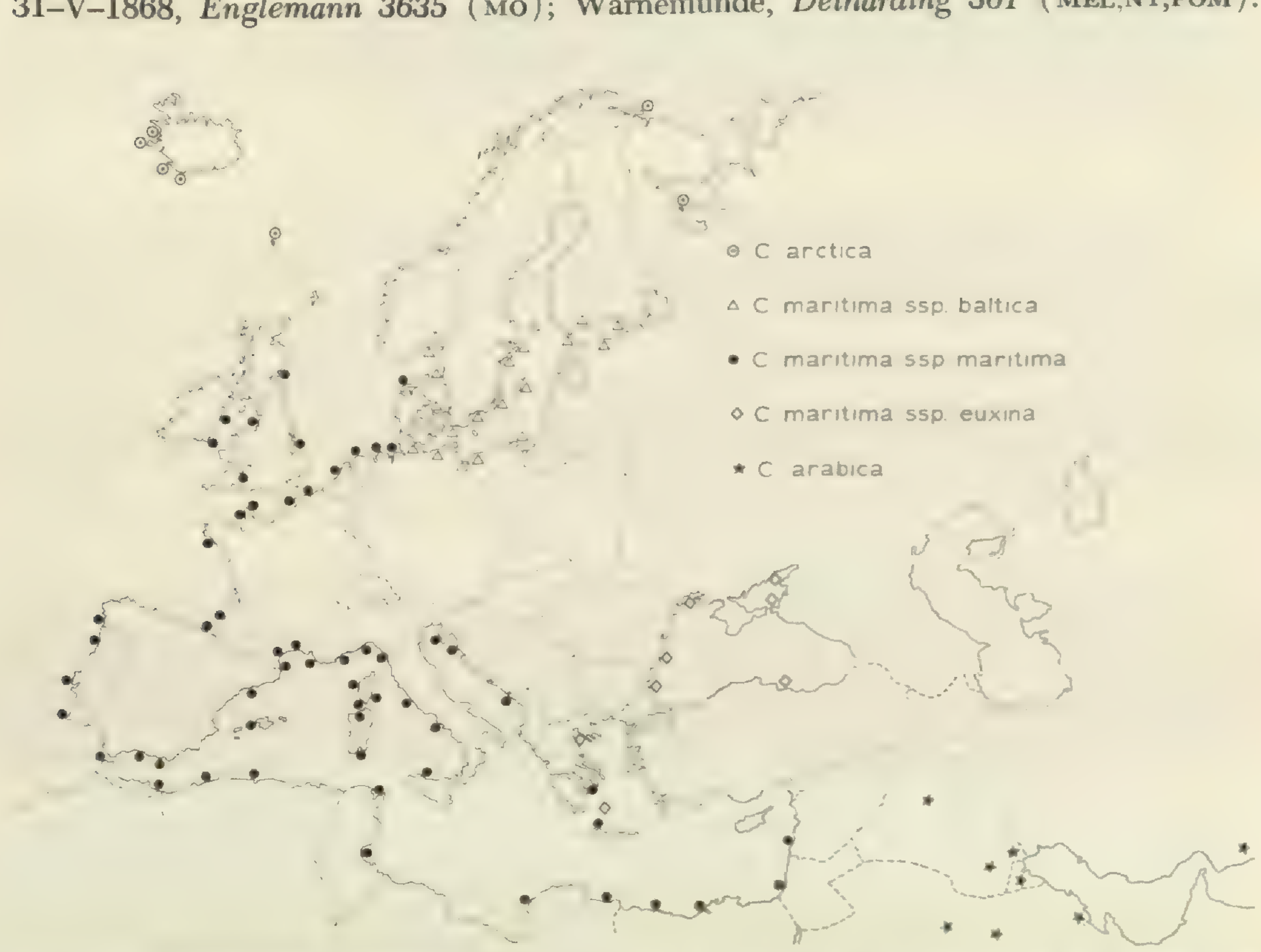
Cakile baltica Jord. ex Pobed., Not. Syst. Leningrad 15: 66. 1953. Holotype: U.S.S.R., "Prov. Kaliningradskaja, distr. Maritimus, Kurskaja kossa (Kurisch–Nerung) prope dunam Schwarzerberg, ad sinum Kurisch," 16–VII–1949. *Pobedimova & Ratnitzina 1216* (LE, not seen).

Cakile maritima var. *bipinnata* O. E. Schulz in Urb., Symb. Antill. 3: 504. 1903, *pro parte*. Syntypes: "Hab. ad mare balticum prope Pillau, in Turcia, Graecia." (?B; not seen).

Leaves deeply and finely pinnatifid, the lobes and rachis rarely more than 4 mm wide, the lobes up to 3 cm long, often 1 cm apart and ± alternate along the rachis, linear to oblanceolate, the lobes of large leaves often further lobed, sinuately to laciniately; leaves seemingly not as fleshy as in typical subspecies; fruiting pedicels divergent to reflexed, 3–5 mm long, 1–2 mm wide; mature fruit ± hastate, usually constricted at the point of articulation; the lower fruit segments conical, expanding toward the apex, the lateral horns usually 1–2 mm long, the articulating surface ± flat across to slightly convex; upper fruit segments mitriform to obconical, weakly 4-angled to terete, apex acute to blunt, the base with a scarious border. CHROMOSOME NUMBER: $2n=18$.

DISTRIBUTION: sandy shores of the Baltic Sea and the Kattegat and Skagerrak channels. Flowering from June to October.

REPRESENTATIVE SPECIMENS. **Denmark.** Sjaelland, Dragsholm, 16–VII–1862, *Leth s.n.* (DS); Jutland, Alrø, 20–IX–1964, *Larsen 63* (BRI,DS). **Estonia.** Rakvere coast, 12–VIII–1934, *Meinertzhagen s.n.* (BM). **Finland.** Alandia, Storrevet, 13–VII–1911, *Johansson 695* (MO,NY,UC); Karelia, Haapasaari, 14–VII–1937, *Kohonen s.n.* (NCU); Nylandia, Helsinki, 13–VIII–1961, *Oinonen s.n.* (FSU); near Hanko, 2–VIII–1964, *Alava 4469* (UC); Satakunta, Luvia, 12–IX–1965, *Kause & Seikkula s.n.* (UC). **Germany.** Greifsvalde, IX–1933, *Guyot s.n.* (NY); Kiel, 1827, *Meyer s.n.* (MO); Rugen, 31–V–1868, *Englemann 3635* (MO); Warnemunde, *Detharding 361* (MEL,NY,POM).



MAP 1. Distribution of *Cakile arctica*, *C. maritima* ssp. *baltica*, ssp. *maritima*, and ssp. *euxina*, and *C. arabica* in the Old World (probable occurrence of *C. arctica* in Spitsbergen and of *C. maritima* in the Canaries not indicated; range of *C. maritima* where naturalized not mapped).

Poland. Hel, Jastarnia, 22–VIII–1937, *Trela s.n.*(US); Wolin, 1949, *Kobendza s.n.* (DAO). **Sweden.** Goteborg, Wargo, VIII–1904, *Thedenius s.n.* (MICH,PH); Gotland, Ljugarn, 20–VII–1941, *Fries s.n.* (DAO); Halland, Vallda, 13–VII–1934, *Skottsberg s.n.* (UC); Skane, Falsterbo, 10–IX–1964, *Hekking 3469* (NSW); Sodermanland, Asko, 24–VIII–1926, *Asplund 861* (DAO,NCU,NY).

Rouy and Foucaud's (1895) name for the Baltic Sea plants was published in the rank of "forme," by which term these authors did not mean the *forma* of current usage but a rank more or less intermediate between species and variety, corresponding to the "proles" of Schulz (1903). Two specimens were cited in the protologue, but Ball (1964a), in effecting the subspecies combination adopted here, did not choose a lectotype; indeed, the herbarium of deposit is not known for certain. Pobedimova (1953) legitimately published Jordan's (1864) *nomen nudum* as *Cakile baltica* Jordan ex Pobed. and specified a type in Leningrad. Later, however (1964), she interpreted this species as *C. baltica* (Jordan ex Rouy & Fouc.) Pobed. and cited her type as a neotype, apparently implying that Rouy and Foucaud's specimens were lost or destroyed.

The Baltic Sea plants are not sharply distinct from typical *Cakile maritima*, but they can usually be distinguished by an ensemble of leaf, pedicel, and fruit characters. The leaves are deeply pinnatifid, and there appears to be a trend toward very finely dissected leaves in the eastern end of the Baltic Sea. Pedicels are longer on the average than in typical *C. maritima*, and the fruits are usually smaller and with a flatter articulating surface. The seed glucosinolate composition, with a predominance of allylglucosinolate, is distinctive.

1c. **Cakile maritima** Scop. ssp. **euxina** (Pobedimova) Nyárády

PLATE 1; MAP 1.

Cakile maritima ssp. *euxina* (Pobed.) Nyárády in Savul., Fl. Reip. Pop. Roman. 3: 480. 1955.

Cakile euxina Pobed. in Grossheim, Key Pl. Cauc. 386. 1949. *Nomen nudum.*

Cakile euxina Pobed., Not. Syst. Leningrad 15: 71. 1953. Holotype: U.S.S.R., "Prope oppidum Scadowsk, in litore marino arenoso, ponti Euxini." 15–VIII–1947, *Pobedimova 48* (LE; **not seen**); **isotypes: A,MO,NY,US.**

Cakile maritima var. *bipinnata* O. E. Schulz in Urb., Symb. Antill. 3: 504. 1903, *pro parte.* Syntypes: "Hab. ad mare balticum prope Pillau, in Turcia, Graecia." (?B; not seen).

Leaves finely and deeply pinnatifid, the lobes and rachis 1–4 mm wide, the lobes widely and alternately or irreguarly spaced, rounded at the apex, often further lobed sinuately to laciniately; fruiting pedicels divergent to often nearly appressed, 2–4.5 mm long, 1.5–3 mm wide; mature fruit angulate-ovate in outline, 17–21 mm long, without prominent lateral horns; the lower fruit segment conical, prolonged upward at the articulating surface into 2 sharp-pointed triangular wedges, the surface concave between; the upper fruit segment conical and with a scarious basal margin. CHROMOSOME NUMBER $2n=18$.

DISTRIBUTION: coast of the Black Sea and sporadically on shores of the Aegaean. Flowering from May to September.

REPRESENTATIVE SPECIMENS. **Bulgaria.** Sozopol, 29–VIII–1932, *Stojanoff s.n.* (CAS). **Greece.** Plaka, 31–VIII–1891, *Sintenis & Bornmuller 1161* (PH); 4 miles S. of Salonica, VIII–1918, *Ramsbottom s.n.* (BM). **Romania.** Dobrogea ad Capul Sabla, 13–VI–1925, *Borza & Nyárády 633* (BM,MO,NSW), 27–V–1963, *Morariu s.n.* (CAS). **Turkey.** Samsun, 6–VII–1931, *Krause 3893* (UC). **U.S.S.R.** Azoff, *Gandoger s.n.* (MO); mouth of the Kuban River, 11–VIII–1916, *Woronow 897* (NY); Odessa, *Kelk s.n.* (NY); Strelka, 9–VII–1959, *Kuznetzova s.n.* (NY).

Cakile maritima ssp. *euxina* is poorly represented at least in American herbaria; hence, it is difficult to assess the full range of variation in the Black Sea plants. Hedge (1965) questioned whether the characters delimiting this taxon were clearly related to geographical distribution. The material available to me for study, however, was homogeneous and distinct enough to merit taxonomic separation from typical *C. maritima*. The differences are of degree, however, not kind, and it therefore seems reasonable to adopt the view of Nyárády (1955) and Ball (1964a,b) and treat the Black Sea plants as a subspecies of *C. maritima*, from which they most likely evolved since the late Pliocene.

2. **Cakile lanceolata** (Willdenow) O. E. Schulz

Plants herbaceous to suffrutescent, annual to fortuitously perennial, not especially succulent, erect to more often straggling or prostrate, much-branched, the branches often more than 5 dm long; first leaves up to 4 × 15 cm, broadly ovate or ovate-deltoid and petiolate to ovate-lanceolate and more attenuate basally, ± entire to variously lobed to deeply and finely pinnatifid; later leaves smaller, usually oblanceolate, less lobed; fruiting racemes usually more than 2 dm long, linear or sinuous; pedicels ca. 1 mm wide and 1.5–4 mm long in fruit, divergent; sepals 3.5–5 mm long, dimorphic, bigibbous; petals clawed, 4.9–9.4 mm long and 1.7–4.3 mm wide, white to rarely pale lavender; nectaries conspicuous, the medians 0.3–0.7 mm high; stamens tetradynamous, the anthers 1.1–2.2 mm long, dehiscing introrsely to latrorsely; pistil ensiform to turbinate; stigma capitate; mature fruit subcyclindric and elongated to short and tumescent, 13–31 mm long, weakly 4-angled to terete, striate, or sulcate, the apex usually acute; seeds small, oblong, somewhat compressed longitudinally, accumbent to occasionally incumbent, dimorphic, the upper ones larger and heavier than the lower ones.

KEY TO THE SUBSPECIES

A. Fruit turbinate, the beak less than the length of the seminiferous part. . . . . 2c. *C. lanceolata* ssp. *alacranensis*.

A. Fruit fusiform or lanceolate, the beak equalling or exceeding the length of the seminiferous part. . . . . B.

B. Fruit slenderly lanceolate with a long beak, the upper fruit segment usually twice the length of the lower segment or greater; leaves usually sinuately or dentately lobed. . . . . 2a. *C. lanceolata* ssp. *lanceolata*.

B. Fruit fusiform or lanceolate with a short beak, the upper fruit segment usually less than twice the length of the lower segment; leaves pinnatifid to less commonly sinuately to dentately lobed. . . . . C.

C. Fruit fusiform, ± oval in cross-section and 4(–8)–sulcate. . . . . 2b. *C. lanceolata* ssp. *fusiformis*.

C. Fruit slenderly lanceolate, usually constricted at the point of articulation, weakly 4-angled to terete. . . . . 2d. *C. lanceolata* ssp. *pseudoconstricta*.

2a. **Cakile lanceolata** (Willd.) O. E. Schulz ssp. **lanceolata**

Plate 1; Map 2.

Raphanus lanceolatus Willd., Sp. Pl. 3: 562. 1800. Holotype: "Antillis," *anon. s.n.* (B, not seen; photo: GH).

Cakile lanceolata (Willd.) O. E. Schulz in Urb., Symb. Antill. 3: 504. 1903.

Cakile domingensis Tussac, Fl. Ant. 1: 119. Pl. 17. 1808. Type: Dominican Republic, Port Francois, (?) *Tussac s.n.* (?P; not seen).

Cakile lanceolata ssp. *domingensis* (Tussac) O. E. Schulz in Urb., Symb. Antill. 3: 505. 1903.

Cakile aequalis L'Hér. ex DC., Reg. Veg. Syst. Nat. 2: 430. 1821. Holotype: Martinique, *Richard s.n.* (G; seen on microfiche: IDC 800. 89: I. 8.).

Cakile maritima var. *aequalis* (DC.) Chapman, Fl. S. U.S. 31. 1860.

Cakile americana var. *cubensis* DC., Reg. Veg. Syst. Nat. 2: 429. (May) 1821. Lectotype: Cuba, Cayo Bonito, *Humboldt & Bonpland s.n.* (P; seen on microfiche: IDC 6209. 119: I. 3.).

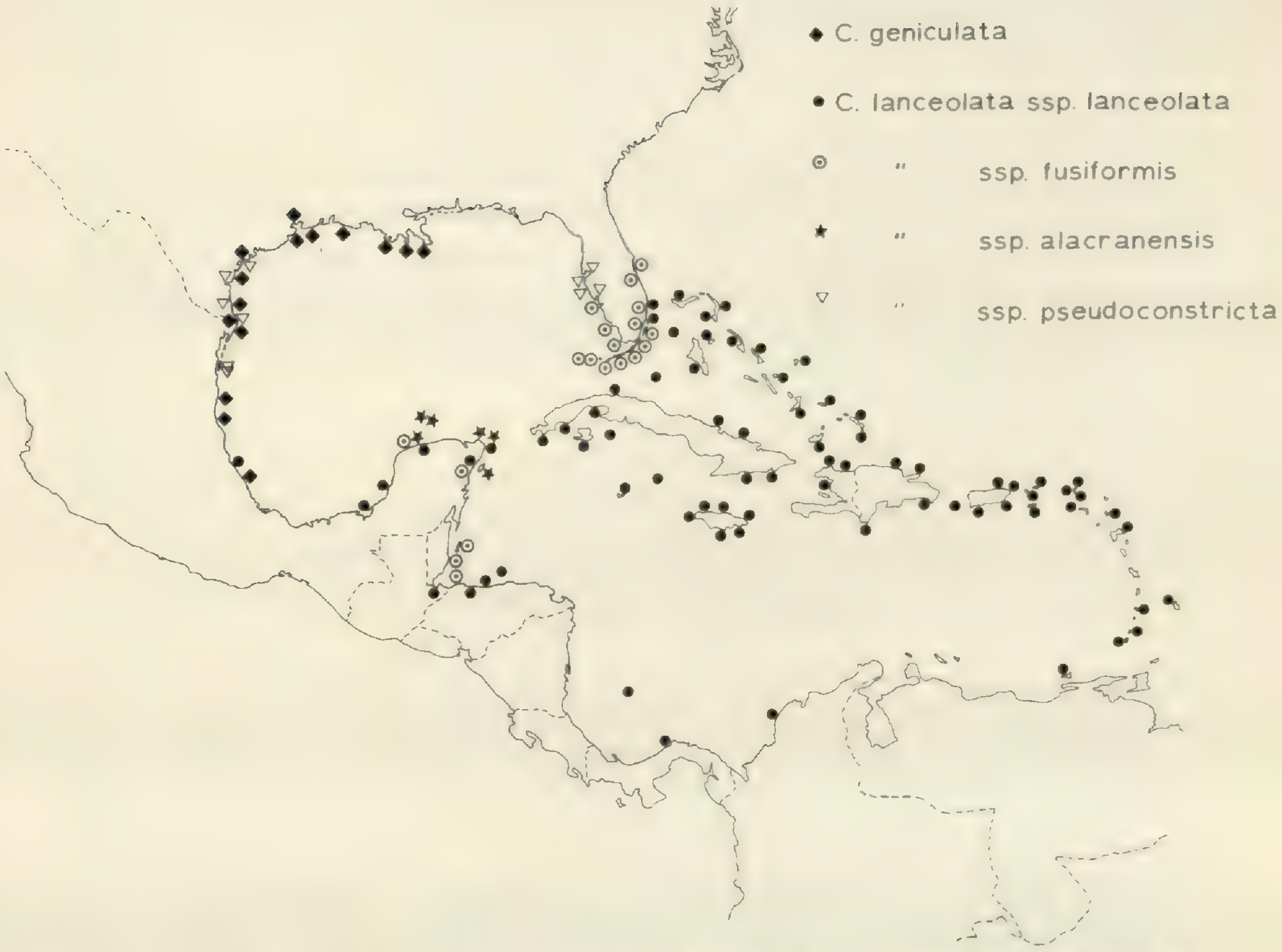
Cakile maritima var. *cubensis* (DC.) Chapman, Fl. S. U.S. ed. 2, Suppl. 606. 1883.

Cakile cubensis Kunth in HBK, Nov. Gen. Sp. Pl. 5: 75. (Sept.) 1821. Holotype: Cuba, Cayo Bonito, March 1801, *Humboldt & Bonpland s.n.* (P; seen on microfiche: IDC 6209. 119: I. 3.).

Plants usually diffuse, sprawling, with branches often more than 1 m long; leaves ovate to lanceolate, sinuately to dentately lobed to rarely pinnatisect; fruiting racemes usually more than 3 dm long; fruiting pedicels 1.5–4 mm long; sepals 4–5 mm long, dimorphic, bigibbous; petals clawed, 5.4–9 mm long and 1.7–4.3 mm wide, white to rarely pale lavender; mature fruit 19–31 mm long, the upper segment usually more than twice the length of the lower segment, long-beaked, ± lanceolate, usually not constricted at the point of articulation of the 2 segments; lower fruit segment 5–10 mm long, terete basally, expanded toward apex into an oval surface, often with 2 small teeth projecting upward; upper fruit segment slenderly conical, weakly tetragonal or furrowed, broadest at the base, the apex acute to less often blunt, the beak occasionally curved. CHROMOSOME NUMBER: $2n=18$.

DISTRIBUTION: sandy beaches of the Greater and Lesser Antilles, the Bahamas, Bermuda, and the Carribbean Coast of Venezuela, Colombia, and Central America; sporadic in southernmost Florida and the Mexican coast of the Gulf of Mexico. Flowering throughout the year.

REPRESENTATIVE SPECIMENS. **Anguilla.** Island Harbour, 3–I–1959, *Proctor 18613* (BM,IJ,US). **Bahamas. Acklin's Island,** Atwood Cay, 4–XII–1907, *Wilson 7423* (F,GH, K,NY); **Andros Island,** Little Golden Cay, 6–III–1966, *Dawson 26700* (GH,US); **Grand Bahama Island,** Russell Town, 31–III–1969, *Gillis 7788* (GH); **Great Abaco,** Cook's Cove, 6–VIII–1953, *Robertson 24* (DS); **Inagua,** 18–X–1904, *Nash & Taylor 1155* (F, NY); **Mayaguana,** Abraham Bay, 8–XII–1907, *Wilson 7531* (F,GH,NY); **New Providence,** West Bay, 26–II–1946, *Degener 18924* (GH,NY,PH); Salt Key Bank, Water Key, 22–V–1909, *Wilson 8144* (F,MO,NY); San Salvador near French Bay, 19–III–1963, *Gillis 5257* (DUKE,IJ,MSC); **South Bimini Island,** 28–III–1965, *Stimson 1061* (DUKE,GA, GH,MICH,SMU,TEX,UC); South Caicos, 16–XII–1907, *Wilson 7660* (F,GH,NY). **Barbados.** Hastings, VI–1895, *Waby 31* (BM,F,K,US). **Bermuda.** Tucker's Town, 20–IX–1905, *Brown & Britton 314* (F,K,NY,PH,US). **Colombia.** Cartagena, XII–1964, *Sarmiento 55* (COL,US). **Cuba.** Camaguey, Punta Arenas, 9–III–1909, *Shafer 698* (F,NY,US); **Isle of Pines,** Caleta, 8–III–1916, *Britton, Wilson & Leon 15284* (F,NY,US). **Dominican Republic.** Beata Island, 7–VIII–1950, *Howard 12444* (BM,GH,IJ,MICH). **Guadeloupe.** East of Moule, 9–XI–1959, *Proctor 19888* (BM,IJ,US). **Haiti. Tortue Island,** 31–XII–1928, *Leonard & Leonard 11396* (GH,NY,US). **Honduras.** La Ceiba, 6–VII–1938, *Yuncker, Koepper & Wagner 8237* (BM,F,GH,K,MICH,MO,NY,US). **Jamaica. Grand Cayman,** 6–VIII–1962, *Sauer 3334* (WIS); St. Anne's Bay, 27–III–1908, *Harris 10353* (BM, F,K,NY,US); **St. James Parish,** near Little River, 14–VIII–1963, *Crosby & Anderson*



MAP 2. Distribution of *Cakile geniculata* and *C. lanceolata* ssp. *lanceolata*, ssp. *fusiformis*, ssp. *alacranensis*, and ssp. *pseudoconstricta* in the New World (occurrence of *C. lanceolata* in Bermuda not indicated).

1195 (DUKE,F,GH,MICH,MSC,NY,RSA,UC). **Mexico. Campeche:** Isla Aguada, 11–VII–1962, *Sauer & Gade 3182* (MICH). **Quintana Roo:** Tancah, 5–VIII–1932, *Steere 2516* (MICH). **Panama.** Viento Frio, 8–VIII–1911, *Pittier 4113* (GH,NY,US). **Puerto Rico.** Cabo Rojo, 9–II–1885, *Sintenis 591* (BM,F,GH,MSC,NY,US); Culebra, 12–III–1906, *Britton & Wheeler 206* (F,NY,US); Santurce, 23–I–1899, *Heller & Heller 256* (CU,F,K, NY,US). **U.S.A. Florida: Dade Co.,** Key Biscayne, 7–IX–1959, *Atwater 138* (FLAS); **Palm Beach Co.,** Lake Worth, 3–V–1941, *Cummings s.n.* (FLAS). **Martin Co.,** Jupiter Island, 30–IX–1962, *Lakela 25422A* (LAF,NCU,SMU,USF); **Venezuela.** Without locality, 1859, *Cruger s.n.* (K). **Virgin Islands. St. Croix,** 11–XI–1895, *Ricksecker 68* (DS,F,GH, MO,NY,UC,US); Tortola, 16–XII–1918, *Fishlock 272* (GH,K,PH).

The Caribbean and West Indian sea rockets were for a century known by the name *Cakile aequalis* L'Hér. ex DC. until Schulz (1903) resurrected Willdenow's earlier name. While Schulz specified that the type was from "Antillis," the Berlin specimen (a photograph of which was very kindly provided me by Dr. Th. Eckardt) carries a label reading "Habitat in Guinea (w)." If this label belongs with the specimen, the plant could have originated from the Guianas (which would then represent a range extension southeast from Barbados and Venezuela) or less likely from African Guinea. *Cakile* could have been transported in ship ballast during

the slave trade, but this seems doubtful because it is otherwise completely unknown from the coast of tropical Africa.

Minor but real variation characterizes many island collections of *Cakile lanceolata*, apparently as a result of local isolation or small population effects. Two somewhat distinctive examples include the Cayman Islands, where the plants tend toward pinnatifid leaves and short-beaked fruits, and Bermuda, with fleshy plants with short-beaked, somewhat tetragonal fruits. The differentiation of what are here interpreted as subspecies of *C. lanceolata* appears to be an intensification of the pressures isolating these rather distinct island forms.

2b. **Cakile lanceolata** (Willd.) O. E. Schulz ssp. **fusiformis** (Greene) Rodman comb. nov.

PLATE 1; MAP 2.

Cakile fusiformis Greene, Pittonia 3: 346. 1898. Holotype: Florida, "Mangrove Key," 10–III–1898, *Pollard 19* (ND–G); isotypes: F,NY,US.

Cakile lanceolata var. *fusiformis* (Greene) Patman, Quart. Jour. Fla. Acad. 25: 198. 1962. Basionym not cited, hence illegitimate.

Cakile alacranensis × *aequalis* Millsp., Field Mus. Bot. 2: 130. 1900. Holotype: Florida, Palm Beach Co., Palm Beach, 28–XII–1895, *Webber 243* (MO); isotype: F.

Cakile Chapmanii Millsp., Field Mus. Bot. 2: 130. 1900. Lectotype: Florida, Dade Co., Miami, VII–1877, *Garber 6472* (US); isotypes: F,PH.

Leaves ovate-lanceolate, nearly entire to dentately lobed to most commonly pinnatifid; fruiting pedicels 2–4 mm long; sepals 4–5 mm long, distinctly bigibbous; petals distinctly clawed, 4.9–9.4 mm long and 2.4–4.2 mm wide, white to very rarely pale lavender; median nectaries 0.4–0.7 mm high; anthers 1.3–1.8 mm long; mature fruit 16–25.5 mm long, 4–6 mm wide, broadly to slenderly fusiform, striate to sulcate (4–8 striae or sulci), somewhat compressed longitudinally; lower fruit segment 5–10 mm long, narrowly terete basally and expanded into a broad oval articulating surface, usually with 2 small teeth projecting upward; upper fruit segment 10.5–18 mm long, ± tumescent, tapering somewhat abruptly to an acute beak, the basal margin scarious. CHROMOSOME NUMBER: $2n=18$.

DISTRIBUTION: sandy coast of the Bay of Honduras from Honduras to the Yucatan Peninsula and southern Florida. Flowering throughout the year.

REPRESENTATIVE SPECIMENS. **British Honduras.** Stann Creek, 7–I–1932, *Schipp 284* (F,MO,UC); Turneffe Islands, Deadman II Cay, 10–IV–1962, *Stoddart 127* (IJ,US). **Honduras.** Cortez, Travesia, 30–V–1970, *Hernandez & Barkley 40488* (herb. of Northeastern University); Tela, 8–V–1919, *Blake 7279* (US). **Mexico. Quintana Roo:** Tancah, 5–VIII–1932, *Steere 2519* (MICH). **Yucatan:** Progreso, 15–VIII–1932, *Steere 3114* (MICH,SMU). **U.S.A. Florida: Broward Co.,** Ft. Lauderdale, XI–1903, *Small & Carter 951* (PH); **Collier Co.,** Marco Island, 25–XII–1961, *Duncan 21854* (GA,LAF,NCU); **Dade Co.,** Key Biscayne, 4–VI–1966, *DeBoer 44* (NCU,USF); Miami Beach, 11–I–1930, *Moldenke 385* (DUKE,MO,NY,US); **Indian River Co.,** Indian River, 1874, *Palmer 12* (F, GH,MO); **Lee Co.,** Sanibel Island, 9–III–1954, *Cooley 2560* (FLAS,GH,MICH,NY,USF); **Manatee Co.,** Bradentown, 4–III–1935, *Weber s.n.* (FLAS); **Monroe Co.,** Knights Key,

30–IV–1896, *Curtis 5645* (F,FLAS,GH,MO,MSC,NY,POM,UC); Marquesas Keys, IV–1886, *Curtis 198* (BM,F,GH,NY,PH,US); **Palm Beach Co.,** Palm Beach, 3–V–1969, *Cassen 470* (FLAS).

The southern and western Florida sea rockets present a nightmare of variation to the taxonomist. A number of epithets have been applied to these plants *(aequalis, cubensis, fusiformis, Chapmanii),* but Patman (1962) recently considered all southern and western Florida material to be *Cakile lanceolata* var. *fusiformis.* Both herbarium collection studies and field work indicate that there is enough geographic integrity to certain morphologically recognizable characters to justify the formal recognition of three taxa in this area: *C. constricta* to the north, *C. lanceolata* ssp. *fusiformis* primarily in the Florida Keys, and *C. lanceolata* ssp. *pseudo-constricta* between. This necessitates the unfortunate synonymization of Millspaugh's (1900) *C. Chapmanii,* which has been widely but varyingly used for over 50 years. Millspaugh cited eight collections in the protologue without designating a specific type. I have studied all eight collections, and one, *Garber s.n.* (US #6472), bears the annotation by Millspaugh: "Cakile Chapmani [sic] sp. nov. Type C. F. Millspaugh." This collection most closely, though not perfectly, conforms to the original description, and I feel compelled to designate it as the lectotype of the name. This specimen, from Miami, Florida, is clearly indistinguishable from *C. fusiformis* Greene (1898), and consequently, *C. Chapmanii* becomes, as here lectotypified, a synonym of *C. lanceolata* ssp. *fusiformis.* Pobedimova (1964) treated *C. Chapmanii* (without designating a type) as a synonym of *C. cubensis,* a name which, after study of the type material in Paris (seen on microfiche), I consider synonymous with *C. lanceolata* ssp. *lanceolata.* Indeed, Pobedimova annotated two sheets of *Brown & Britton 314* (US) from Bermuda as *C. lanceolata* and *C. cubensis* although I can see no differences between them.

In the original description of *Cakile fusiformis,* Greene (1898) characterized the lower fruit segments as sterile. Millspaugh (1900) and Small (1903) confounded things by describing the lower segments as 2-spermous and using this feature as a key character. As Pobedimova (1964) pointed out, however, the fruit segments are typically one-seeded. In any large population sample some 2(-3)-spermous or aborted lower segments will be encountered.

Cakile lanceolata ssp. *fusiformis* can be distinguished from other *C. lanceolata* plants by its fusiform fruits which have a somewhat bloated appearance and which are commonly 8-striate or 8-sulcate longitudinally. The taxon occurs disjunctly in southern Florida and on the coast of the Bay of Honduras to the Yucatan Peninsula where it intergrades with *C. lanceolata* ssp. *lanceolata* to the south and *C. lanceolata* ssp. *alacranensis* to the north and where it may have originated by hybridization between these two taxa.

2c. **Cakile lanceolata** (Willd.) O. E. Schulz ssp. **alacranensis** (Millspaugh) Rodman comb. nov.

PLATE 1; MAP 2.

Cakile alacranensis Millsp., Field Mus. Bot. 2: 130. 1900. Lectotype: Mexico, Alacran Shoals, Pajaros Island, 8–III–1899, *Millspaugh 1764* (F).

Cakile lanceolata var. *alacranensis* (Millsp.) O. E. Schulz in Urb., Symb. Antill. 3: 506. 1903.

Cakile edentula var. *alacranensis* (Millsp.) O. E. Schulz, Pflanzenreich IV, 105: 27. 1923.

Leaves ovate to lanceolate, petiolate to attenuate basally, sinuate to dentate to shallowly lobed; fruiting racemes 2–3 dm long, usually congested; fruiting pedicels thin, 2–3.5 mm long; sepals 3.5–5 mm long; petals clawed, 6.2–7 mm long and 1.9–2.6 mm wide; median nectaries 0.3–0.5 mm high; anthers 1.2–1.5 mm long; mature fruit short, turbinate, 14–19 mm long, 5–7 mm wide, with 4 thin striae or sulci running longitudinally to the acute apex; lower fruit segment 5–6 mm long, narrowly cylindric basally and expanded into a broad oval articulating surface, occasionally with 2 small teeth projecting upward; upper fruit segment 9–13 mm long, nearly globose but for the short, acute beak, slightly compressed longitudinally, striate or sulcate.

DISTRIBUTION: sandy coast and offshore islands of the Yucatan Peninsula.

REPRESENTATIVE SPECIMENS. **Mexico. Quintana Roo:** Puerto Juarez, 19–VII–1962, *Sauer & Gade 3270* (F); **Isla Mujeres,** 1–I–1895, *Millspaugh 13* (GH,MICH); **Cozumel Island,** 11–VI–1885, *Gaumer 139* (F,GH,K). **Yucatan.** Alacran Islands, 8–III–1899, *Millspaugh 1767* (F), 30–VI–1961, *Fosberg 41864, 41868, 41900* (DUKE,US,USF); Progreso, IV–1887, *Millspaugh 7* (F).

Cakile lanceolata ssp. *alacranensis* is distinguished by its plump, turbinate fruits. It is endemic to the coast of the Yucatan Peninsula and nearby islands, including the Alacrans. Sauer (1967), who has done field work in this area, thought it likely that the Alacran plant was a "seaborne immigrant from the Yucatan Peninsula upstream." Furthermore, Sauer (1967) described sandy beaches of Quintana Roo with "a nearly continuous row of sea rocket, *Cakile alacranensis*." While plants of *C. lanceolata* ssp. *lanceolata* and *C. lanceolata* ssp. *fusiformis* have been collected in this region, *C. lanceolata* ssp. *alacranensis* would appear to form a series of populations, especially in the northern part of the peninsula, with sufficient geographic integrity to justify the recognition of a discrete subspecies. In fruit morphology the plants intergrade with *C. lanceolata* ssp. *fusiformis* but appear to have somewhat smaller flowers and a distinctive seed glucosinolate composition (based upon a single sample).

2d. **Cakile lanceolata** (Willd.) O. E. Schulz ssp. **pseudoconstricta** Rodman ssp. nov.

PLATE 1; MAP 2.

Folia pinnatifida profunde; folia prima ad 3 × 12 cm, folia serotiniara parviora oblanceolata ± integra; pedicelli divergentes 1.5–5 mm longi; sepala lanceolata 4–5 mm longa bigibbosa; petala unguiculata, 6–8.2 mm longa × 2–2.8 mm lata, alba vel

lavandula raro; nectaria mediana 0.3–0.6 mm alta; antherae 1.2–1.7 mm longae; siliculae lanceolatae 15–24 mm longae constrictae plerumque ad locum articuli; articulus inferior 5.5–8 mm longus cylindricus vel conicus leviter ± teris; articulus superior tenuis 9–17 mm longus, 3–4 mm latus, fusiformis vel conicus, teris vel tetragonus apice acuto et labio basali exiguo.

Holotype: Florida, Hillsborough Co., "sea-shore," 6–III–1904, *Fredholm 6324* (GH); isotypes: MO,US.

DISTRIBUTION: coastal strand of southwestern Florida, Texas, and Tamaulipas. Flowering throughout the year.

REPRESENTATIVE SPECIMENS. **Mexico. Tamaulipas:** Laguna Madre, 2–XII–1939, *Le Sueur 150* (TEX), 20–VI–1962, *Sauer & Gade 2933* (WIS). **U.S.A. Florida: Hillsborough Co.,** Egmont Key, 8–IV–1969, *Long 2901* (USF); **Lee Co.,** Boca Grande, 12–III–1952, *Field & Lazar s.n.* (F,GA,US); **Manatee Co.,** Anna Maria Key, 12–IV–1917, *Cuthbert 1533* (FLAS); **Pinellas Co.,** Redington Beach, 20–V–1962, *Patman 1088* (BM, GH,USF); **Sarasota Co.,** Longboat Key, 20–XI–1964, *Godfrey 65244* (FSU). **Texas: Aransas Co.,** Goose Island State Park, 11–X–1960, *Traverse 1774* (GH,SMU,TEX); **Brazoria Co.,** Freeport Beach, 20–IV–1952, *Killip 42102* (US); **Cameron Co.,** Padre Island, 16–III–1929, *Tharp 5573* (NY,TEX,US); **Nueces Co.,** Corpus Christi, 11–III–1917, *Palmer 11246* (MO,POM,TEX,UC); **San Patricio Co.,** 8 miles S. of Taft, 2–VII–1951, *Jones 590* (SMU); **Willacy Co.,** Port Mansfield, 1–V–1959, *Traverse 1185* (F,MO,SMU, TEX,US).

The plants here treated as *Cakile lanceolata* ssp. *pseudoconstricta* have usually been identified with *C. lanceolata* ssp. *fusiformis* because of their pinnatifid leaves, showy flowers, and sprawling habit of growth. However, the plants develop fruits similar to and often indistinguishable from those of *C. constricta* which typically possesses fleshy, ± entire leaves and smaller flowers. *Cakile lanceolata* ssp. *pseudoconstricta* is the predominant sea rocket on the Gulf of Mexico strand of south-central Florida and also occurs sympatrically with *C. geniculata* in Texas and Tamaulipas. I interpret this sympatry as a secondary phenomenon, most likely arising from the recent introduction of these plants probably in ship ballast from the Tampa Bay region of Florida. The taxon may have evolved during the Pleistocene on islands of what was, during periods of higher sea level, southern Florida.

3. **Cakile edentula** (Bigelow) Hooker

Succulent, herbaceous to rarely suffrutescent annuals (or fortuitous perennials), usually erect, up to 8 dm, much-branched, the branches spreading and ascending, the lowermost ones often decumbent, the stems, sometimes purplish; first leaves very fleshy and thick, broadly ovate and petiolate to obovate or spatulate and attenuate at the base, crenately, sinuately, or dentately lobed, never pinnatifid, up to 7 × 15 cm; later leaves smaller, ± oblanceolate, less lobed; lobing of leaves most pronounced at basal, petiolar end; fruiting racemes 1–2 dm long, rarely longer, usually congested, linear to slightly geniculate; pedicels divergent in fruit, 1–2 mm wide, 1.5–8 mm long; sepals ovate, the laterals scarcely gibbous at the base, the apex often with sparse simple trichomes; petals ± obovate, not distinctly clawed, 4.6–9.7 mm long, 1.4–3.3 mm wide, white to pale lavender; petals frequently absent or present only as small white bristles, especially early in the season; nectaries very small, the medians 0.2–0.4 mm high; stamens at first tetradynamous, becoming nearly equal as flower ages, anthers 0.4–1.4 mm long, dehiscing introrsely; pistil lanceolate to ± turbinate; stigma capitate to sunk

in retuse beak; mature fruit 12–29 mm long, 4-angled or 8-ribbed, beaked, the beak ± flattened in one plane and acute, blunt, or retuse at the apex, the point of articulation of the two segments usually ± constricted; lower fruit segment terete, ± cylindric to expanded slightly toward apex; upper fruit segment truncate-fusiform to turbinate, 4-angled or 8-ribbed; seeds ellipsoid to oblong, dimorphic; cotyledons accumbent to occasionally incumbent.

KEY TO THE SUBSPECIES

A. Upper fruit segment 4-angled; articulating surface of lower fruit segment ± flat to concave and with 2(6) small teeth projecting upward. . . 3a. *C. edentula* ssp. *edentula*.
A. Upper fruit segment 8-ribbed; articulating surface of lower fruit segment flat and without teeth. . . . . 3b. *C. edentula* ssp. *Harperi*.

3a. **Cakile edentula** (Bigel.) Hook. ssp. **edentula**

KEY TO THE VARIETIES

A. Upper fruit segment plump, 5–9 mm wide, short-beaked, the beak less than the length of the seminiferous part, the base without a scarious margin. . . . . 3a1. *C. edentula* var. *edentula*.
A. Upper fruit segment slender, 3–5 mm wide, long-beaked, the beak equalling or exceeding the length of the seminiferous part, the base with a slight scarious border. . . . . 3a2. *C. edentula* var. *lacustris*.

3a1. **Cakile edentula** (Bigel.) Hook. var. **edentula**

PLATE 1; MAPS 3, 4, 5.

Bunias edentula Bigel., Fl. Bost. 157. 1814. Lectotype: Massachusetts, Boston, *Bigelow 43* (LINN; seen on microfiche: IDC 5073. 529: II. 7.).

Cakile edentula (Bigel.) Hook., Fl. Bor.–Amer. 1: 59. 1830.

Cakile lanceolata ssp. *edentula* (Bigel.) O. E. Schulz in Urb., Symb. Antill. 3: 504. 1903.

Cakile americana Nutt., Gen. N. Amer. Pl. 2: 62. 1818. Syntypes: ". . . on the strand of the sea-coast, and also on the shores of the great North Western Lakes of the St. Lawrence." (?BM; not seen) *pro parte*.

Cakile maritima var. *americana* (Nutt.) Torrey, Comp. Fl. N. Middle States 246. 1826.

Cakile geniculata × *edentula* Millsp., Field Mus. Bot. 2: 127. 1900. Holotype: New York, Staten Island, *Kearney s.n.* (NY); isotype: F.

Cakile lanceolata var. *Millspaughii* O. E. Schulz in Urb., Symb. Antill. 3: 506. 1903. A new name for the preceding.

Cakile edentula var. *Millspaughii* (O. E. Schulz) O. E. Schulz, Pflanzenreich IV, 105: 26. 1923.

Cakile lanceolata var. *apetala* O. E. Schulz in Urb., Symb. Antill. 3: 506. 1903. Holotype: New York, Staten Island, *Rabenau s.n.* (?B; not seen).

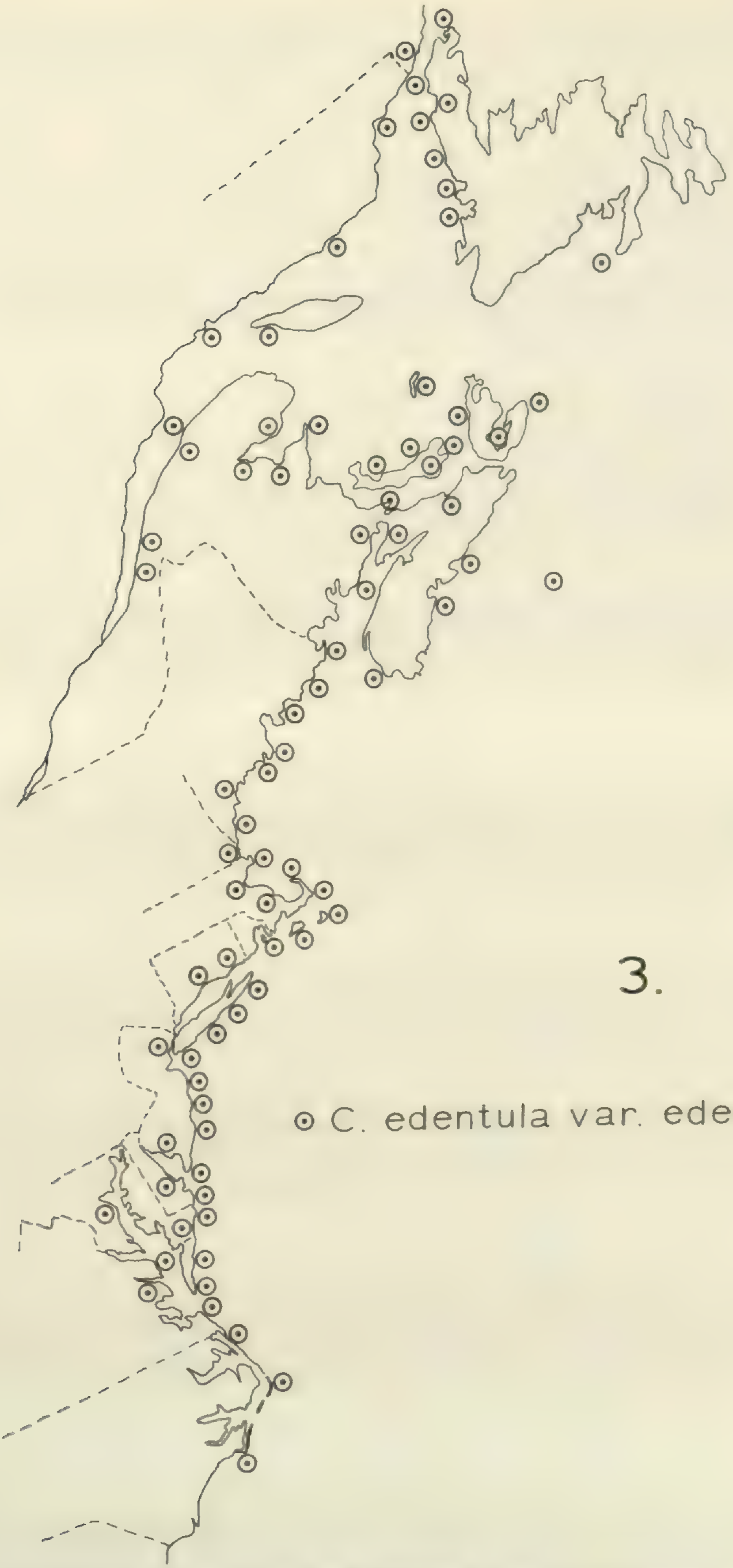
Cakile edentula subvar. *apetala* (O. E. Schulz) O. E. Schulz, Pflanzenreich IV, 105: 27. 1923.

Cakile californica Heller, Muhlenbergia 3: 10. 1907. Lectotype: California, beach at Monterey, 29–VI–1903, *Heller 6856* (GH); isotypes: DS,F,MO,NY,PH,POM,UC,US.

Cakile edentula var. *californica* (Heller) Fern., Rhodora 24: 23. 1922.

Cakile edentula ssp. *californica* (Heller) Hult., Lunds Univ. Arsskr. II. Sect. 2. 41: 824. 1945.

Cakile lanceolata var. *australiensis* Thell. in Hegi, Ill. Fl. Mittel–Eur. 4: 183. 1916. Type: none specified.



MAP 3. Distribution of *Cakile edentula* var. *edentula* in eastern North America (excluding Great Lakes; range of *C. edentula* where naturalized not mapped).

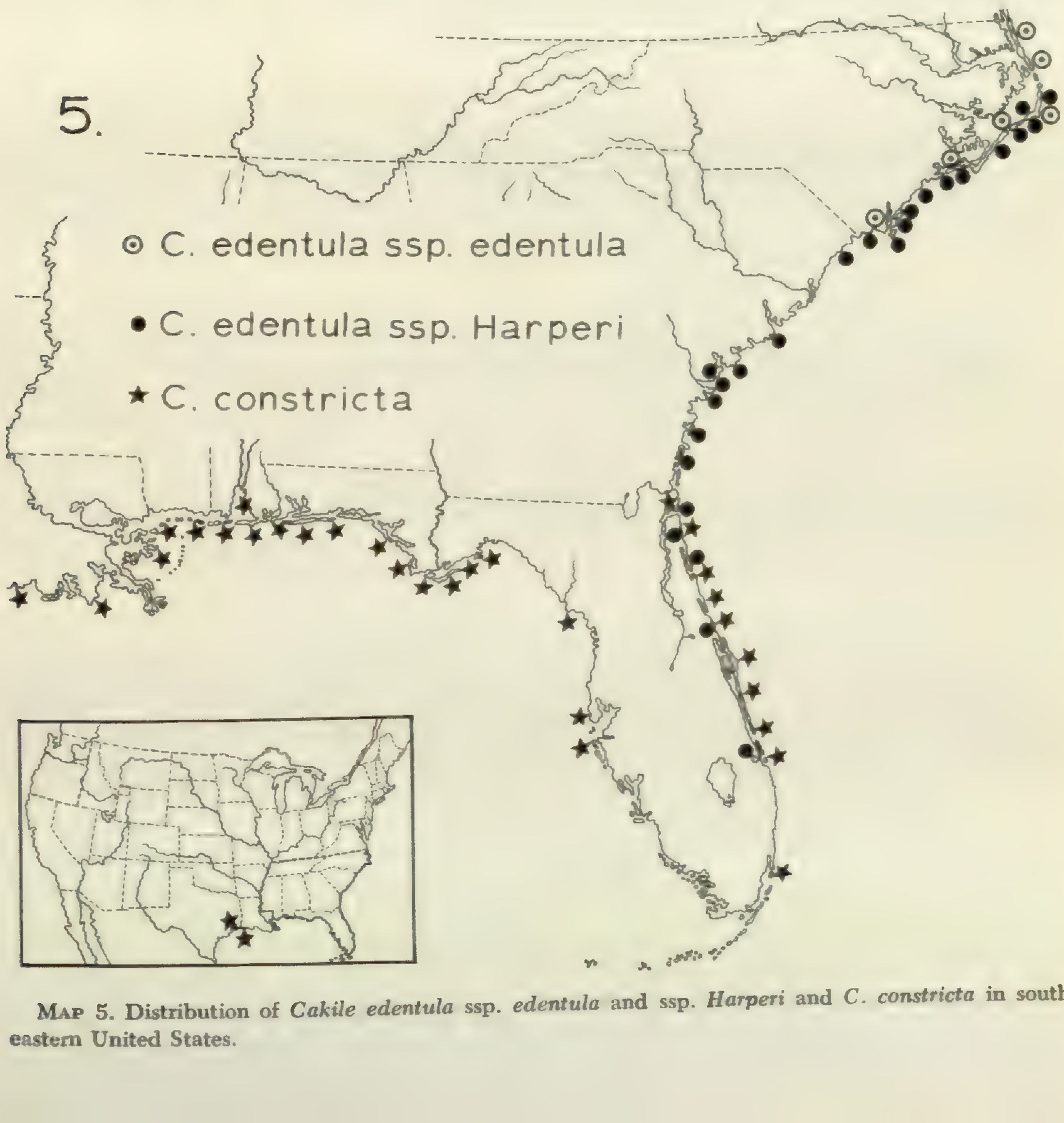
Map 4. Distribution of *Cakile edentula* var. *edentula* and *C. edentula* var. *lacustris* in the Great Lakes region.

Plants fleshy, usually erect, much-branched, the branches smooth to weakly striate or sulcate, sinuous to flexuous; fruiting racemes 1–2 dm long, rarely to 3 dm, linear to somewhat flexuous; fruiting pedicels 1.5–8 mm long, 1–2 mm wide, divergent; sepals 3.5–5 mm long, dimorphic, the laterals 1.2–1.5 mm wide, the medians 1.5–2 mm wide; petals 4.6–7.9 mm long and 1.4–3.3 mm wide (on the Pacific Coast: 5.5–9.7 mm long and 1.4–3.2 mm wide), often fewer than 4 or reduced to bristles; anthers 0.4–1.4 mm long, dehiscing introrsely; mature fruit 12–24 mm long, 4–8 mm wide, somewhat turbinate, slightly constricted at the point of articulation; the lower fruit segment terete, cylindric, expanded slightly toward apex, 5–10 mm long, the articulating surface ± flat to concave, usually with 2(6) small teeth projecting upward or the sides prolonged upward into 2 opposite triangular wedges; upper fruit segment 7–15 mm long, 4-angled and occasionally with 4 additional weak ridges between the ribs, beaked, the beak short, compressed longitudinally, acute to retuse at the apex; seeds large, ellipsoid, dimorphic. CHROMOSOME NUMBER: $2n=18$.

DISTRIBUTION: coastal beaches from southernmost Labrador, the Gulf of St. Lawrence, and the St. Lawrence River east of Quebec, to the Outer Banks of North Carolina; sporadic on the shores of Lakes Michigan, Erie, and Ontario; naturalized on the Pacific Coast of North America and the shores of temperate Australia; occasionally introduced as a ballast weed. Flowering from June to November in its native range.

REPRESENTATIVE SPECIMENS (native range). **Canada. Labrador:** Forteau, *Fernald & Wiegand 3476* (CU,GH). **New Brunswick:** Bathurst, *Blake 5393* (GH,K,US); **Campobello Island,** *Smith s.n.* (UC,US). **Newfoundland:** Cow Head, *Fernald & Wiegand 3475* (GH, K,NY); Frenchmans Cove, *Mackenzie & Griscom 10295* (GH); Main Gut Bridge, *Rouleau 6425* (DAO,FSU,GH,NY,US). **Nova Scotia: Cape Breton Co.,** Scatari Island,

Smith et al. 5249 (DAO); **Cumberland Co.,** South Cove E. of Joggins, *Barrington* 388 (GH); **Sable Island,** *St. John 1241* (GH,K,NY,PH,US). **Prince Edward Island:** Cape Aylesbury, *Fernald, Long & St. John 7511* (GH,PH); Souris, *Erskine 1444* (DAO). **Quebec:** Blanc Sablon, *Fernald, Wiegand & Long* 28314 (GH,PH); **Gaspé Co.,** Riviere a Claude, *Dore & Jones 17308* (DAO); Magdalen Islands, Hospital Pond, *Fernald et al. 7510* (GH,PH); Rimouski, *Basset & Crompton 4266* (DAO). **U.S.A. Connecticut: Fairfield Co.,** Greens Farms, *Pollard 128* (US); **New Haven Co.,** New Haven, *Young* 198 (OSU); **New London Co.,** Norwich, *Setchell s.n.* (NY). **Delaware: Kent Co.,** Woodland Beach, *Commons s.n.* (PH); **New Castle Co.,** ½ mile S. of River-Bay Monument, *Larsen 1022* (GA,PH); **Sussex Co.,** 5 miles S. of Rehoboth Beach, *McVaugh 6513* (F,GH,NY). **Maine: Cumberland Co.,** Cape Elizabeth salt marsh, *Seymour 20125* (SMU); **Hancock Co.,** Seal Harbor, Mt. Desert Island, *Redfield 5108* (MO,PH); **Knox Co.,** Port Clyde, *Friesner 1121* (CAS,DUKE,F,NY,SMU); **Lincoln Co.,** Monhegan Island, *Jenney, Churchill & Hill s.n.* (MO); **Sagadahoc Co.,** Hermit Island, *Salamun 191* (WIS); **Waldo Co.,** Islesboro, *Rossbach 3520* (NCU); **Washington Co.,** Jonesport, *Peabody s.n.* (GH); **York Co.,** York, *Blake s.n.* (NY,PH). **Maryland: Anne Arundel Co.,** Sandy Point, *Ewan 17374* (CAS,GH); **Calvert Co.,** Scientists Cliffs, *Seymour 16789* (SMU,WIS); **St. Marys Co.,** Millstone, *Tidestrom 5136* (MICH); **Talbot Co.,** Deep Water Point, *Earle 3817* (PH); **Worcester Co.,** Ocean City, *Fogg 11448* (GH). **Massachusetts: Barnstable Co.,** Provincetown sand dunes, *Goodale s.n.* (DUKE); **Dukes Co.,** Gay Head, Marthas Vineyard, *Carter s.n.* (PH); **Essex Co.,** Ipswich, *Oakes s.n.* (F,GH,PH); **Nantucket Co.,** N. shore beach, *Pennell 11160* (PH); **Plymouth Co.,** Plymouth Beach, *Fernald, Hunnewell & Long* 9545 (PH); **Suffolk Co.,** Revere Beach, *Forbes s.n.* (POM,TEX,UC). **New Hamp-**



MAP 5. Distribution of *Cakile edentula* ssp. *edentula* and ssp. *Harperi* and *C. constricta* in southeastern United States.

shire: Rockingham Co., beach at Rye, *Miller 5621* (GH). **New Jersey: Atlantic Co.,** Atlantic City, *Letterman s.n.* (NY,PH); **Cape May Co.,** Cape May, *Gershoy 325* (CU, GH); **Cumberland Co.,** S. of Bayside, *Long 44480* (PH); **Middlesex Co.,** South Amboy, *Mackenzie 2235* (MO); **Monmouth Co.,** Avon, *Selby s.n.* (OSU); **Ocean Co.,** Mantaloking, *Muenscher 43* (CU,GH); **Salem Co.,** S. of Elsinboro Point, *Fogg 10140* (PH). **New York: Brooklyn Co.,** Marine Park, *Muenscher & Curtis 6174* (CU); **Kings Co.,** Rockaway Beach, *Svenson 8071* (SD); **Nassau Co.,** Jones Beach, *Gleason & Smith 152* (BM, CU); **Richmond Co.,** Staten Island, *Small s.n.* (F,NY,US); **Suffolk Co.,** Montauk Point, *Moldenke & Moldenke 10655* (MO,NY,POM,SMU). **North Carolina: Brunswick Co.,** Southport, *Ahles & McCrary 58377* (NCU,SMU); **Carteret Co.,** Beaufort, *Blomquist 10387A* (DUKE,GH); **Currituck Co.,** Kitty Hawk, *Godfrey 5274* (GH,US); **Dare Co.,** Hatteras salt marsh, *Radford 45106* (LAF,NCU,TEX,WIS); **Hyde Co.,** Ocracoke Island, *Mathews s.n.* (NCU). **Rhode Island: Kent Co.,** Warwick, *Congdon s.n.* (POM); **Newport Co.,** Block Island, *Fernald & Long 9544* (GH,PH); **Washington Co.,** Narragansett, *Williamson s.n.* (PH). **Virginia: Accomack Co.,** S. end of Assateague Island, *Iltis 24110* (SMU,WIS); **Hampton Co.,** Hampton, *Seymour 91715* (DUKE); **Lancaster Co.,** Windmill Point, *Edwin 389* (FSU); **Middlesex Co.,** Urbanna, *Hermann 10426* (GH); **Norfolk Co.,** near Ocean View, *Kearney 1225, 1448* (US); **Northampton Co.,** west of Kiptopeke, *Fernald, Long & Fogg 5309* (GH,PH); **Princess Anne Co.,** Virginia Beach, *Heller s.n.* (PH); **Warwick Co.,** Newport News, *Bartram s.n.* (PH); **Westmoreland Co.,** Camp Potomac, *Iltis 148* (SMU).

REPRESENTATIVE SPECIMENS (naturalized or introduced). **Azores.** Fayal, 11–VIII–1894, *Brown 8* (GH,MO), VIII–1956, *C.U. 124* (BM). **Australia. New South Wales:** Between Botany Bay and Sydney Head, XII–1871, *Daintree s.n.* (MEL); Currarong, 7–X–1960, *Constable s.n.* (A,NSW); Hat Head, E. of Kempsey, 18–I–1953, *Constable 22487* (NSW,US); Jerseyville, VI–1910, *Boorman s.n.* (NSW); Lord Howe Island, Salmon Beach, 16–VII–1967, *Balgooy 1000* (CANB,NSW); Port Macquarie, II–1927, *Evans s.n.* (PH). **Queensland:** Broadbeach, 2 miles S. of Southport, 10–VI–1969, *McDonald 435* (BRI); Deception Bay, 13–XI–1932, *White 8684* (BRI,UC); Heron Island, 5–X–1960, *Fosberg 41300* (NY,US); Palm Beach between Currumbin and Tallebudgera Creeks, 15–XI–1929, *White 6571* (A,BRI,NY); Stradbroke Island, VII–1922, *White 1680* (BRI,NSW). **South Australia:** Beachport, 1–XII–1917, *Black s.n.* (AD); Fowler's Bay, 12–IX–1960, *Wilson 1598* (AD); Head of Great Australian Bight, 6–I–1971, *Orchard 3195* (AD); Kangaroo Island, D'Estrees Bay, XII–1881, *Tate s.n.* (AD); Victor Harbour, II–1921, *Cleland s.n.* (AD). **Tasmania:** Kings Island, 1882, *Spong s.n.* (MEL); Port Davey, 14–III–1954, *Davis 1304* (A). **Victoria:** East Gippsland, 15–VIII–1944, *Willis s.n.* (MEL); Point Lonsdale, XI–1903, *Cowle 38* (MEL); Port Fairy, VI–1904, *Maiden s.n.* (NSW); Queenscliffs, 29–VII–1867, *Mueller s.n.* (MEL); Warrnambool, XI–1898, *Williamson s.n.* (MEL). **Western Australia:** Delisser Sandhills, 26–XI–1967, *Parsons 8* (AD); Eucla, 22–II–1967, *Symon 4685* (AD,NSW). **Canada. British Columbia:** Queen Charlotte Islands, Moresby, 29–VIII–1946, *Cowman s.n.* (UBC); Vancouver Island, vicinity of Ucluelet, 7–VIII–1909, *Macoun 78288* (GH,NY). **New Zealand.** North Island, Raumati Beach, 20–XII–1958, *Ashwin 710* (CAS,SMU); Stewart Island, Butterfield Beach, 21–II–1935, *Philson, Doore & Earle 340* (GH). **U.S.A. Alaska:** Kodiak Island, Three Saints Bay, 5–VIII–1931, *Eyerdam 525* (BM,CAS,DS); Middleton Island, 3–VIII–1956, *Thomas 6360* (DS,US); Yakutat, 14–VII–1945, *Stair s.n.* (PH). **California: Alameda Co.,** beach at West Berkeley, VII–1882, *Greene s.n.* (GH); **Del Norte Co.,** Crescent City, 19–IX–1912, *Eastwood 2281* (CAS); **Humboldt Co.,** Samoa, 7–VIII–1901, *Tracy 1266* (UC); **Los Angeles Co.,** Anaheim Landing, 7–X–1930, *Fosberg 53174* (NY); Marin Co., beach near Bear Valley, 9–IX–1897, *Eastwood s.n.* (F); **Mendocino Co.,** Fort Bragg, 1914, *Mathews 161* (UC); **Monterey Co.,** Monterey Bay, 1887, *Hickman s.n.* (ND–G); **Orange Co.,** Newport, 7–IX–1907, *Davidson 1770* (DS); **San Diego Co.,** San Diego, VI–1906, *Brandegee s.n.* (NY,UC,US); **San Francisco Co.,** San Francisco, 11–VII–1893, *Congdon s.n.* (DS); **San Luis Obispo Co.,** Morro sand dunes, 23–V–1908, *Condit 22* (UC); **San Mateo Co.,** Spanish Town, 1893, *Dudley s.n.* (DS); **Santa Barbara Co.,** Surf, V–1902, *Elmer 3628* (DS,GH,MO,NY,US); **Santa Cruz Co.,** Capitola, 4–VIII–1894, *Burnham s.n.* (CU); **Sonoma Co.,** Bodega Bay, 21–VII–1932, *Purer 4040* (SD); **Ventura Co.,** Ventura, 17–IV–1916, *Eastwood 5024* (CAS). **Illinois: Cook Co.,** Lake Shore, 12–VII–1891, *Moffat 162* (WIS). **Indiana: Porter Co.,** Mineral Springs, 6–IX–1911, *Wolcott 71* (F).

Michigan: Berrien Co., St. Joseph, 27–IX–1949, *Jordal 2431* (MICH); **Mason Co.,** Ludington, 25–VII–1959, *Miller & Milstead 169* (NCU). **New York: Erie Co.,** "Shore Lake Erie," *Kneiskern s.n.* (NY). **Oregon: Clatsop Co.,** Clatsop Spit, XI–1902, *Stubenrauch s.n.* (UC); **Coos Co.,** Charleston Bay, 6–V–1911, *Smith 3667* (F,NY); **Curry Co.,** Rogue River, VIII–1917, *Hawkins s.n.* (WIS); **Lane Co.,** W. of Florence, 28–VIII–1949, *Cronquist 6104* (CAS,GH,MICH,NY,RSA,SMU,UC,US); **Lincoln Co.,** Newport, 1917, *Hawkins s.n.* (WIS); **Tillamook Co.,** Nestucca, VIII–1901, *Kirkwood 123* (NY). **Washington: Clallam Co.,** Port Angeles, 26–VI–1908, *Flett 3381* (US); **Grays Harbor Co.,** Copalis, XI–1911, *Foster 1534* (NY,US); **Island Co.,** Deception Pass State Park, 30–VII–1936, *Smith 1384* (UC); **Jefferson Co.,** Pt. Hadlock, VII–1931, *Jones 3279* (PH); **Pacific Co.,** Long Beach, 13–VIII–1907, *McGregor s.n.* (DS); **San Juan Co.,** Argyle, 1–VIII–1917, *Zeller & Zeller 866* (GH,MO,NY,US); **Whatcom Co.,** Pt. Roberts, 9–VII–1937, *Muenscher 7896* (CU). **Wisconsin: Kenosha Co.,** Kenosha, 11–IX–1932, *Wadmond s.n.* (WIS); **Manitowoc Co.,** Point Beach State Park, 2–IX–1962, *Clarke 3–2* (WIS); **Milwaukee Co.,** Atwater Beach, 24–VII–1939, *Shinners 629* (SD); **Sheboygan Co.,** Cedar Grove, 21–IX–1958, *Iltis 12732* (WIS).

Ball (1964a) expressed doubt about recognizing *Cakile edentula* as being distinct from *C. maritima*. His argument was based on the assumption that the Icelandic sea rockets represented a subspecies of *C. edentula*, which would encompass a range of variation for several characters overlapping that of *C. maritima*. The Icelandic plants, however, constitute a distinct species; when they are excluded, *C. edentula* remains easily distinguishable from *C. maritima* on the basis of vegetative, floral, and fruit morphology and breeding system.

The southern limit of *Cakile edentula* var. *edentula* on the Outer Banks of North Carolina corresponds closely to the influence of the Labrador Current which reaches southward nearly to Cape Hatteras (Cotter 1965). A number of coastal plants with which typical *C. edentula* is associated, such as *Ammophila breviligulata* and *Hudsonia tomentosa*, also reach their southern limits on the Outer Banks (cf. Radford, Ahles & Bell 1968). The range of *C. edentula* var. *edentula* thus appears to correspond to a natural biogeographic area, at least for coastal organisms, which is undoubtedly strongly influenced by coastal currents.

Recently, Patman (1962) reported *Cakile edentula* var. *edentula* from Indian River, St. Johns, Santa Rosa, Volusia, and Wakulla counties in Florida. The plants probably are *C. constricta*, which is vegetatively similar to *C. edentula* var. *edentula* but has larger flowers and much thinner fruits. Sporadic, ballast plants of *C. edentula* would not be wholly unexpected, however.

Within populations of typical *Cakile edentula*, on both the Atlantic and Pacific coasts, one usually finds a varying proportion of plants with very purplish stems and young fruits and purple petals. Marie-Victorin (1935) early pointed this out and suggested that nomenclatural recognition be accorded these plants. However, since they appear to represent only color morphs within populations, they deserve nothing more than *forma* status if any. I have the impression, gained from my field work, that the proportion of purplish forms increases northward on both coasts, but it would require a more thorough population study to document this.

3a2. **Cakile edentula** (Bigel.) Hook. var. **lacustris** Fernald

PLATE 1; MAP 4.

Cakile edentula var. *lacustris* Fern., Rhodora 24: 23. 1922. Holotype: Indiana, Lake Co., Millers, 4–IX–1911, *Sherf s.n.* (GH); isotype: F.

Cakile edentula ssp. *lacustris* (Fern.) Hult., Lunds Univ. Arsskr. II. Sect. 2. 41: 824. 1945.

Cakile lacustris (Fern.) Pobed., Nov. Syst. Pl. Vasc. 1964: 108. 1964.

Plants generally less robust and fleshy than the typical variety; flowers usually with 4 petals; petals 5–7 mm long and 1.5–2.6 mm wide; anthers 0.6–1.3 mm long; fruiting pedicels divergent, 2–8 mm long and 1–2 mm wide; mature fruit 16–26 mm long, 3–5 mm wide, slightly constricted at the point of articulation; lower fruit segment ± terete, cylindric, 5–12 mm long, the articulating surface ± flat and usually with 2 small teeth projecting upward; upper fruit segment 11–18 mm long, 4-angled and occasionally with 4 additional vague ridges between the angles, long-beaked, the beak longitudinally compressed, acute, blunt, or retuse at the apex; seeds oblong or ellipsoid, dimorphic. CHROMOSOME NUMBER: $2n=18$.

DISTRIBUTION: sandy beaches of the Great Lakes of North America and very sporadic on the St. Lawrence River east of Quebec. Flowering from May to October.

REPRESENTATIVE SPECIMENS. **Canada. Ontario:** Ipperwash Beach, 19–VII–1941, *Soper* 2239 (DAO,GH); Picton, 5–IX–1937, *Marie-Victorin & Rolland–Germain 49469* (GH,NSW,TEX); Port Stanley, 26–VIII–1880, *Burgess s.n.* (DAO); Rondeau Provincial Park, 29–VII–1965, *Iltis 24104* (SMU,WIS); Sault Ste. Marie, *Pitcher s.n.* (NY); Shore of Lake Ontario, 28–VII–1868, *Macoun 180* (GH). **U.S.A. Illinois: Cook Co.,** Chicago, 1860, *Scammon 1174a* (F,GH); **Lake Co.,** Waukegan, 28–VIII–1908, *Gates 2976* (F, MICH). **Indiana: Lake Co.,** Whiting, 25–VII–1875, *Hill s.n.* (F); **Laporte Co.,** Michigan City, 7–IX–1903, *Lansing 1901* (F); **Porter Co.,** Dune Park, 22–VI–1896, *Chase 472* (PH). **Michigan: Alcona Co.,** 4 miles N. of Harrisville, 12–VIII–1951, *McVaugh 12520* (MICH); **Allegan Co.,** 2 miles S. of Douglas, 10–X–1948, *Cain, Segadas–Vianna & Hagenah s.n.* (DAO); **Arenac Co.,** Point Lookout, 10–VII–1900, *Wheeler 360* (MSC); **Benzie Co.,** Betsie Point, 16–VIII–1951, *McVaugh 12626* (MICH); **Berrien Co.,** St. Joseph, 10–VIII–1838, *Wright s.n.* (MICH); **Cheboygan Co.,** without locality, 18–VII–1962, *Voss 10977* (MICH); **Delta Co.,** Escanaba, 1–IX–1902, *Schuette 11* (F,US); **Emmet Co.,** Little Traverse Bay, 30–VII–1894, *Selby s.n.* (OS); **Grand Traverse Co.,** Traverse Bay, 23–VIII–1947, *Ball 3054* (US); **Huron Co.,** Port Austin, 28–VII–1896, *Davis s.n.* (MSC); **Marquette Co.,** beach strand at Huron Mountain Club lodge, 12–VIII–1961, *Bourdo 3218* (MSC); **Mason Co.,** Ludington, 1910, *Chaney 212* (F,NY,US); **Monroe Co.,** Monroe, 23–VIII–1914, *Chandler s.n.* (US); **Muskegon Co.,** Muskegon, 3–IX–1963, *Gillis 5408* (MSC); **St. Clair Co.,** N. of Port Huron, 7–IX–1892, *Dodge s.n.* (MICH). **New York: Cayuga Co.,** North Fair Haven, 31–VII–1916, *Munz 657* (CU,POM,UC); **Chatauqua Co.,** Barcelona, 11–VIII–1896, *Churchill s.n.* (MO); **Jefferson Co.,** Woodville, 11–IX–1921, *House 8664* (GH,NY); **Erie Co.,** Buffalo, VIII–1838, *Clinton s.n.* (F,MICH,MSC,NY); **Monroe Co.,** Rochester, 20–VIII–1892, *Manwell s.n.* (CU); **Niagara Co.,** Youngstown, 19–VIII–1911, *Smith 2433* (CAS); **Oswego Co.,** Oswego, VIII–1882, *Wibbe s.n.* (NY); **Wayne Co.,** Sodus Point, 3–VIII–1924, *Killip 12467* (US). **Ohio: Ashtabula Co.,** Ashtabula, 24–VI–1899, *Kellerman s.n.* (OS); **Cuyahoga Co.,** Dover Bay, 13–VIII–1895, *Stair s.n.* (NY); **Erie Co.,** Cedar Point, 21–VIII–1886, *Wilkinson s.n.* (UC); **Lake Co.,** Madison, 23–VIII–1878, *McCall s.n.* (UC); **Lorain Co.,** without locality, 26–IX–1891, *Strong s.n.* (MICH); **Lucas Co.,** Toledo, IX–1929,*Wareham s.n.* (OS); **Ottawa Co.,** Lakeside, 1897, *Simkins s.n.* (OS). **Pennsylvania: Erie Co.,** Erie, 25–X–1864, *Clinton s.n.* (PH). **Wisconsin: Door Co.,** introduced at Foscoro, VIII–1894, *Fellows s.n.* (US); **Green Bay Co.,** Green Bay shore, 2–VII–1898, *Schuette s.n.* (F,GH,NY); **Kenosha Co.,** without locality, 11–VIII–1900, *Wadmond 152* (PH); **Kewaunee Co.,** shore, 30–VII–1892, *Schuette s.n.* (F); **Manitowoc Co.,** Two Rivers, 19–IX–1945, *Benke 6484* (F); **Milwaukee Co.,** Lake shore,

VIII–1841, *Lapham s.n.* (F,MEL,MO,NY,RSA,WIS); **Ozaukee Co.,** Lake Church, 22–VII–1939, *Pohl 1288* (F); **Racine Co.,** Racine, IX–1878, *Davis s.n.* (MO); **Sheboygan Co.,** Sheboygan, 16–VII–1874, *Swezey s.n.* (CAS).

The Great Lakes sea rockets differ from typical *Cakile edentula* primarily in features of the fruit and seed. In many other respects the plants are similar, and consequently, the distinction is here treated at the varietal rank. The two varieties constitute *C. edentula* ssp. *edentula*, believed to be a phyletic unit with the evolution of the Great Lakes variety having occurred following the last glacial maximum.

Cakile edentula var. *lacustris* occurs throughout the Great Lakes but appears to be rare on the shores of Lake Superior. I have seen only a single specimen from this lake in the nearly 400 collections studied. Agassiz (1850) reported "C. americana Nutt." from Lake Superior but made no comments on its abundance. I have seen no collections of *Cakile* from along the St. Lawrence River from Lake Ontario to Quebec City. East of Quebec, *C. edentula* var. *edentula* becomes common, and sporadic plants of *C. edentula* var. *lacustris* probably grow as well (cf. collection 27, Appendix I).

3b. **Cakile edentula** (Bigel.) Hook. ssp. **Harperi** (Small) Rodman comb. nov.

PLATE 1; MAP 5.

Cakile Harperi Small, Fl. S.E. U.S. 478, 1331. 1903. Holotype: Georgia, Chatham Co., Tybee Island, 21–VI–1901, *Harper 923* (NY); isotypes: MO,US.

Plants usually more robust than the typical subspecies, widely branched near the base; fruiting racemes usually 1–2 dm long, occasionally slightly geniculate; fruiting pedicels 2–5 mm long and ca. 2 mm wide; sepals 4–5 mm long, slightly bigibbous; petals 5.5–8 mm long and 1.5–3.2 mm wide; anthers 1.0–1.4 mm long; mature fruit ± cylindric, 20–29 mm long and 4–7 mm wide; lower fruit segment cylindric to expanded slightly toward apex, 7.5–10 mm long, weakly 8-ribbed, the articulating surface ± flat and smooth, rarely with 2 very small teeth, and a slight lip developed around the edge; upper fruit segment ± conical, 12–19.5 mm long, 8-ribbed, beaked, the beak slightly compressed and acute to more commonly retuse at the apex, the articulating surface ± flat; seeds ellipsoid, dimorphic. CHROMOSOME NUMBER: $2n=18$.

DISTRIBUTION: maritime beaches from the Outer Banks of North Carolina south to St. Lucie Co., Florida. Flowering from March to October.

REPRESENTATIVE SPECIMENS. **U.S.A. Florida: Flager Co.,** Flager Beach, 10–IV–1940, *West & Arnold s.n.* (FLAS); **St. Johns Co.,** St. Augustine, III–1869, *Canby s.n.* (NY); **St. Lucie Co.,** Fort Pierce, 9–IV–1904, *Burgess 734* (F,NY); **Volusia Co.,** Enterprise, III–1869, *Canby 156* (F,GH,NY,PH,US). **Georgia: Chatham Co.,** Tybee Island, 8–VI–1958, *Duncan 20813* (LAF); **Glynn Co.,** Jekyll Island, 8–VI–1961. *Boole 1103* (BM, GH,NCU,SMU); **McIntosh Co.,** Sapelo Island, 5–IX–1964, *Turner 138* (NCU). **North Carolina: Brunswick Co.,** Holden Beach, 13–V–1934. *Blomquist 3725* (DUKE); **Carteret Co.,** near Fort Macon. 30–IX–1937, *Blomquist 10209* (DUKE); **Dare Co.,** sand dunes SW. of Hatteras. 23–V–1954, *Radford 8106* (NCU); **New Hanover Co.,** Wrightsville Beach, 2–VI–1962, *Ahles 56605* (GA,GH,NCU,NY,SMU,WIS); **Onslow Co.,** beach at White Oak Creek, 23–V–1941. *Radford & Stewart 1207* (NCU); **Pender**

Co., New Topsail Beach, 2–VI–1962, *Ahles 56608* (FSU,NCU,USF). **South Carolina: Beaufort Co.,** Beach City, 22–VIII–1966, *Bradley 3428* (BM,NCU); **Charleston Co.,** Sullivan's Island, 5–VI–1967, *Bozeman & Logue 9130* (NCU); **Horry Co.,** 3 miles S. of Myrtle Beach, 13–VI–1936, *Correll 5251* (DUKE,GH).

The name *Cakile Harperi* was not treated by Pobedimova (1963, 1964) in her monograph of the genus. Plants of this taxon, which she had borrowed from the Smithsonian, were annotated either as *C. edentula* or *C. geniculata*. The latter has in common with *C. edentula* ssp. *Harperi* a fruit of similar size typically with eight distinct ridges in addition to an overall vegetative similarity in habit and fleshiness. *Cakile edentula* ssp. *Harperi*, however, does not form a distinctly geniculate infructescence and has fruits usually retuse and flattened longitudinally at the apex and with a flat articulation. Its affinities, as Small (1903) indicated, are quite obviously with *C. edentula* ssp. *edentula* from which it differs in having distinctive, larger fruits and larger seeds, a more robust habit, and a different seed glucosinolate composition. The differences, I believe, are substantial enough to justify the recognition of this southern race of *C. edentula* as a subspecies.

The northern limit of the range of *Cakile edentula* ssp. *Harperi* is on the Outer Banks of North Carolina. This also holds for several coastal plants of the southeastern United States, e.g., *Juniperus silicicola, Uniola paniculata, Yucca aloifolia* and *Y. gloriosa, Sabal palmetto, Parietaria floridana, Sesuvium portulacastrum, Croton punctatus,* and *Solanum gracile* (Radford, Ahles & Bell 1968). This northern biogeographic boundary is most likely determined by the eastward deflection of the warm Gulf Stream off Cape Hatteras (Cotter 1965). To the south *Cakile edentula* ssp. *Harperi* becomes less common in northern Florida, being replaced by populations of *C. constricta,* but herbarium collections indicate that it may extend sporadically to just south of Cape Kennedy.

4. **Cakile geniculata** (Robinson) Millspaugh

PLATE 1; MAP 2.

Cakile maritima var. *geniculata* Robins., Syn. Fl. N. Am. 1: 132. 1895. Lectotype: "Coast Matamoros [Tamaulipas, Mexico] to Galveston Bay [Texas]," *Berlandier 3103* (GH); isotypes: F,MO,NY.

Cakile geniculata (Robins.) Millsp., Field Col. Mus. Bot. 2: 126. 1900.

Cakile lanceolata "proles" *geniculata* (Robins.) O. E. Schulz in Urb., Symb. Antill. 3: 506. 1903.

Cakile lanceolata var. *geniculata* (Robins.) Shinners, Field Lab. 20: 33. 1952.

Succulent, herbaceous to occasionally suffrutescent annuals, erect up to 10 dm high, much-branched with branches spreading and ascending; leaves very fleshy, broadly ovate and petiolate to oblanceolate or spatulate, sinuately, dentately, or pinnately lobed; fruiting racemes 1–2 dm long, weakly to usually distinctly geniculate, the pedicels and rachis of nearly equal width and with the fruits widely spaced; pedicels thick, divergent, 2–5 mm long and 1.5–2.5 mm wide in fruit; sepals 3–4 mm long and 1–2 mm wide, scarcely gibbous basally, occasionally with sparse simple trichomes at the apex; petals obovate or spatulate, not distinctly clawed, 4–6.1 mm long and 1.2–

1.9 mm wide, commonly white to pale lavender; nectaries very small, the medians 0.1–0.3 mm high; stamens tetradynamous, the anthers 0.6–1.3 mm long, dehiscing introrsely to slightly latrorsely; pistil lanceolate; stigma capitate; mature fruits lanceolate, 20–27 mm long and 3–5 mm wide, usually distinctly 8-ribbed, acute to more often blunt at the apex, often slightly curved; the lower segment 6–11 mm long, tapered toward the pedicel, weakly 8-ribbed, terete, deeply to shallowly cleft at the apex; the upper segment 13–18 mm long, slenderly conical, with a slight scarious border around the base, the beak acute to blunt at the apex; seed slenderly oblong, dimorphic; cotyledons accumbent to obliquely incumbent. CHROMOSOME NUMBER: $2n=18$.

DISTRIBUTION: sandy strand of Louisiana west of the Mississippi Delta, Texas, Tamaulipas, and Veracruz. Probably flowering throughout the year but with an apparent peak from March to August.

REPRESENTATIVE SPECIMENS. **Mexico. Tamaulipas:** dunes near Miramar, 24–VI–1962. *Sauer & Gade 2962* (WIS); 6 miles S. of "Washington Beach," 4–VI–1955, *Hildebrand & Johnston 2547* (GH). **Veracruz:** Barre de Tuxpan, II–1827, *Berlandier 86* (BM); sandy beach N. of Nautla, VI–1970, *Nevling & Gomez-Pompa 1258* (GH). **U.S.A. Louisiana: Cameron Parish,** 3.5 miles W. of Holly Beach, 17–VI–1968, *Thieret 29350* (A,FLAS,LAF,SMU); **Jefferson Parish,** east end of Grand Isle, 22–IV–1967, *Thieret 25753* (DUKE,FSU,GH,LAF,SMU); **LaFourche Parish,** near Bell Pass, 2–VI–1968, *Lasseigne 1476* (LAF,SMU); **Terrebonne Parish,** Last Island, 8–VI–1913, *Wurzlow s.n.* (NY). **Texas: Aransas Co.,** Aransas Pass, 1922, *Schulz 802* (US); **Brazoria Co.,** 4 miles W. W. of San Luis Pass Bridge, 9–VII–1969, *Rodman 64* (GH); **Cameron Co.,** 2 miles W. of Port Isabel, 28–IV–1959, *Traverse 1150* (F,MO,SMU,TEX,US); **Chambers Co.,** High Island, 11–IV–1957, *Gould 7446* (SMU,UC); **Galveston Co.,** Texas City, 9–IV–1950, *Turner 1820* (SMU); **Willacy Co.,** Port Mansfield, 5–IV–1966, *Crutchfield 1242* (GH).

Robinson (1895) cited two collections, *Berlandier 3103* and *Lindheimer s.n.*, in the protologue of his new variety, and Millspaugh (1900) designated the *Berlandier* collection as "type." There are two sheets of this in the Gray Herbarium, however, one stamped "ex herb. George Thurber"; it is the other sheet, with Berlandier's note of "Coast Matamoros [to] Galveston Bay," which I am designating the lectotype.

Robinson (1895) remarked that the upper fruit segments of the plants possess a retuse beak, but this is not at all characteristic. He had annotated a collection from Enterprise, Florida, made by William Canby as *Cakile maritima* var. *geniculata*, and it was certainly this specimen which Robinson recalled when he wrote of the retuse character. However, this collection is of *C. edentula* ssp. *Harperi* which typically develops a retuse beak. These plants never form the conspicuously geniculate infructescence which distinguishes *C. geniculata* from all other sea rockets.

Mohr (1897) stated that *Cakile geniculata* occurred east of the Mississippi Delta in Alabama, but I have not seen any specimens to substantiate this claim. The collections by Mohr from Alabama which I have studied are all of *C. constricta*. The Delta region separates the ranges of these two species, with *C. constricta* to the east and *C. geniculata* to the west, perhaps because the silty, muddy shores of this area and recurrent flooding constitute barriers to migration. Some overlap occurs, however, for mixed populations are encountered on the coast of western Louisiana and easternmost Texas. Assuming that sea-dispersal of upper fruit

segments is essential for the migration of *Cakile*, one would predict this pattern of overlap since the coastal currents in this northern part of the Gulf of Mexico flow primarily westward (Curray 1965, Otvos 1970). Penetration to the west by seaborne disseminules of *C. constricta* is thus to be expected. Whether the present situation reflects a stable balance between the colonizing potential of each species or constitutes an early step in the westward expansion of the range of *C. constricta* can not be resolved from the record of herbarium collections.

In the western part of the Gulf of Mexico the coastal currents flow northward and, with the westward currents, converge on Padre Island (Curray 1965). This pattern of currents and their climatic effects perhaps restrict *Cakile geniculata* to the northwestern sector of the Gulf. The northward coastal currents might also bring migrants from the south and southeast, which would explain the sporadic occurrence of *C. lanceolata* in Veracruz and Tamaulipas. My field work in Texas in the summer of 1969 revealed the frequent occurrence of mixed populations of *C. geniculata* and *C. lanceolata* ssp. *pseudoconstricta*. The latter, I think, has been repeatedly introduced into this region in ships' ballast from its native range around Tampa Bay and southward in Florida.

5. **Cakile arabica** Velenovsky & Bornmüller in Bornmüller

PLATE 1; MAP 1.

Cakile arabica Velen. & Bornm. in Bornm., Repert. Sp. Nov. 9: 114. 1911. Holotype: "In Arabiae mediae districtu Nefud ad Slih," 1909, *A. Musil s.n.* (PR; not seen).

Plants annual, somewhat fleshy, erect to 6 dm, much-branched, the branches glabrous to occasionally sparsely pubescent; leaves broadly ovate in outline, to 10 cm long, deeply and finely pinnatifid, the lobes few and remote, often further pinnately lobed, acute to obtuse at apex, the lobes and rachis 1–4 mm wide, usually sparsely to densely pubescent with long, simple, white trichomes; flowering racemes elongating in fruit, 1–3 dm long, linear to occasionally weakly geniculate; pedicels appressed, divergent, or reflexed, 1.5–3 mm long in fruit, thin; sepals ovate, ca. 4 mm long, 1.5–1.8 mm wide, slightly dimorphic, the laterals narrower and basally gibbous, often with sparse simple trichomes near apex; petals unguiculate to obovate, 7.8–11.6 mm long and 1.9–3.1 mm wide, pale to deep purple; median nectaries 0.2–0.5 mm high; anthers 1.3–1.6 mm long; pistil long, slender, and terete; stigma large and capitate; mature fruit slenderly ensiform, 14–21 mm long, 2–3 mm wide, sharp-beaked; the lower segment 3–5 mm long, terete, the small articulating surface with two prominent conical teeth 1–2 mm long, projecting upward; the upper segment linear, 10–16 mm long, acute at apex, somewhat 4-angled, with two small lateral bulges at the base and the articulating surface with two distinct pits corresponding to the teeth on the lower segment.

DISTRIBUTION: in sand or gravel deserts of northeastern Saudi Arabia, Kuwait, south Iraq, and southwestern Iran. Flowering from December to April (a single collection in flower and fruit made in August).

REPRESENTATIVE SPECIMENS. **Iraq**. Al-Ichrish, 15–IV–1955, *Guest & Al-Rawi 14191* (K); ca. 30 km S. of Tall Lahm, 30–III–1956, *Guest & Mahallal 15306* (K); Jebel Samara, 23–VIII–1919, *Watson s.n.* (K); Jebel Sanam, II–1919, *Graham 419* (BM), 6–III–1961, *Chakravarty, Rawi, Khatib & Tikrity 29894* (K). **Kuwait.** Arafjan, III–1933, *Dickson 27 bis* (K); without locality, *Fitzgerald 15528/3* (BM). **Saudi Arabia.** Dhahran, 8–III–1940, *Snyder 30* (UC), 2–XII–1947, *Schreuder s.n.* (UC); Great

Nefud between Hail and Linah, 18–III–1966, *Hemming* 2435 (BM); Jabal al-'Amudah, 22–III–1968, *Mandaville Jr. 1733* (BM); Jabal al-Ba'al, 25–I–1968, *Mandaville Jr. 1166* (BM); Jebal Amuda-Mishaal, 7–IV–1949, *Dickson* 543 (K); Jibal an-Nu'ay-riyah, 26–I–1968, *Mandaville Jr. 1184* (BM); Nejd, Saiyiarat, 27° 10′ N., 44° 50′ E., 23–II–1946, *Fitzgerald 15466/1* (BM); 2 km E. of J. Ghuraymil, 8–III–1969, *Mandaville Jr. 1449* (BM); 33 km SE. of Abu Hadriyah, 23–III–1968, *Mandaville Jr. 1810* (BM).

This species, the only inland taxon in the genus, is the least known because of the paucity of collections. Pobedimova (1963, 1964) acquired no material of *Cakile arabica* and had to rely on the indequate published descriptions for her monograph (she also mistakenly attributed the type to Berlin). Consequently, the salient aspect of its morphology–the leaf pubescence–remained unappreciated until quite recently. The type specimen was described as glabrous, but 18 of the 19 collections with vegetative material which I borrowed for study exhibited a sparse to dense pubescence of white trichomes on the undersurface of the leaves. These included a specimen from the Nefud (*Hemming 2435*, BM), the general type locality. Although Rechinger (1964) described Iraqi plants as glabrous, Hedge (1968) stated that "the material from Lower Iraq shows a clear indumentum especially on the ventral surface of young leaves." Hedge (1968) also reported the species for the first time in Iran, from Makran, and mentioned that the single, "rather inadequate" specimen was glabrous. Leaf pubescence may be variable in this species and is perhaps least apparent in older, fruiting plants.

Plants of *Cakile arabica* grow in desert regions in sand or gravel at elevations from near sea level to 2400 feet. A number of collections made by James P. Mandaville, Jr. bear the observation that the plants grow in "sand on limestone." A few collections indicate that at some localities the plants are common, and Halwagy and Macksad (1972) stated that the species is "not uncommon in Kuwait." While never a true strand plant, *C. arabica* has been collected "growing on slopes of hill 200 yds. from seashore" [of the Persian Gulf] (*Dickson 543*, K). The region where the species grows was apparently completely covered by the Tethys Sea into Miocene times (Kummel 1970), and I believe *C. arabica* probably evolved following the regression of water from this region, possibly in the late Miocene.

6. Cakile arctica Pobedimova

Plate 1; Map 1.

Cakile arctica Pobed., Not. Syst. Leningrad 15: 64. 1953. Holotype: USSR, "Archangelsk in insula Solovetzkii, in arena litorali," 17–VII–1890, *Birulja s.n.* (LE; not seen).

Cakile maritima f. *islandica* Gandog., Bull. Soc. Bot. Fr. 47: 343. 1900. Holotype: Iceland, *Jönsson 602* (?LY; not seen).

Cakile edentula f. *islandica* (Gandog.) O. E. Schulz, Pflanzenreich IV, 105: 26. 1923.

Cakile edentula ssp. *islandica* (Gandog.) Löve & Löve, Bot. Not. 114: 52. 1961.

Cakile edentula var. *islandica* (Gandog.) Löve, Taxon 19: 300. 1970.

Cakile lanceolata f. *pygmaea* O. E. Schulz in Urb., Symb. Antill. 3: 507. 1903. Holotype: Iceland, *Wender s.n.* (?B; not seen).

Cakile lapponica Pobed., Not. Syst. Leningrad 19: 44. 1959. Holotype: USSR,

"Peninsula Rybaczii, pagum Tzyp-Navolok," 15–VIII–1956, *Pobedimova, Stanisczeva & Drozdova 442* (LE; not seen); isoyptes: A,MO,WIS.

Fleshy, herbaceous, glabrous annuals, erect to often prostrate, much-branched, the branches spreading; leaves very succulent, broadly ovate and petiolate to obovate, oblanceolate, or spatulate, sinuately to dentately lobed especially basally, up to 3 × 9 cm; fruiting racemes 1–2 dm long, linear; pedicels divergent, ca. 1 mm wide and 5–10 mm long in fruit; sepals 4–5 mm long, 2–3 mm wide, usually glabrous, the outer laterals slightly gibbous at the base; petals clawed, 5.3–9.4 mm long, 2.3–5.3 mm wide, white to purple; median nectaries 0.3–0.5 mm high; stamens tetradynamous, anthers 1.0–1.4 mm long, dehiscing introrsely to latrorsely; pistil lanceolate; stigma capitate; mature fruits large, plump, long-beaked, constricted at the point of articulation of the two segments, 21–31 mm long, 4–6 mm wide, soft-corky in texture; the lower fruit segment 6–11 mm long, broadly cylindric to nearly orbicular, terete, the articulating surface rather flat and smooth; the upper fruit segment 14–20 mm long, terete, plump, tapering to a long acute beak, often curved, the surface smooth to weakly veined; seeds large, dark brown, ellipsoid, dimorphic; cotyledons usually accumbent. CHROMOSOME NUMBER: $2n=18$ (Plate 3).

DISTRIBUTION: sandy coasts of Iceland, the Faeroes, northern Scandinavia to the White Sea, and probably sporadic in Spitsbergen. Flowering from June to October.

REPRESENTATIVE SPECIMENS. **Faeroes.** Insula Suderö, Kvalbö fiord, 2–VIII–1895, *Simmons 281* (MO), 20–VII–1897, *Hartz & Ostenfeld s.n.* (GH). **Iceland.** Grótta, 1–IX–1949, *Löve & Löve A0224* (GH,K); Reykjavik, 19–VIII–1938, *Scamman 1380* (GH,US); Sudurnes, 4–VI–1946, *Löve A0223* (K); Westmann Islands, Klauf-Heimaey, lava beach, 7–VIII–1950, *Crosby-Browne s.n.* (BM,DAO). **U.S.S.R.** "Prov. Archangelsk, insulae Solovetskii, insula Anzer, sinus Kirillovskaja et insula Solovetskij Bolschoj, sinus Peczag, in arenis litoralibus," 21 & 27–VII–1957, *Pobedimova & Kolomojtzeva 4574* (A,MO,WIS).

My interpretation of the Icelandic and Arctic European sea rockets conforms closely to that of Pobedimova (1963, 1964), but I am treating her two taxa, *Cakile arctica* and *C. lapponica*, as a single species, *C. arctica*. The only difference between the two lies in flower size, the type of *C. arctica* having much smaller petals than Icelandic and northern Scandinavian material. Additional specimens from the type region, however (*Pobedimova & Kolomojtzeva 4574*, A,MO,WIS), possess flowers intermediate in size, thus eliminating any discontinuity. If a taxonomic distinction were to be made between these White Sea plants and the rest, I believe it should only be at the rank of variety or form. The plants are otherwise similar vegetatively and in fruit morphology.

This taxonomic view conflicts with the long-standing notion that the Icelandic sea rockets are conspecific with or closely related to typical *Cakile edentula* of North America (Fernald 1922, Schulz 1923, Löve & Löve 1947, 1956). Ball (1964a) summarized opinions on this problem and concluded from his herbarium studies that ". . . although the Icelandic and Arctic European plants have larger petals than typical *C. edentula* (6–12 mm), the fruit closely resembles this species in all respects." My own studies, based on considerably more herbarium material, completely negate this conclusion. *Cakile arctica* and *C. edentula* var. *edentula* differ significantly in pedicel and fruit length (see section on morphology and anatomy), fruit shape (Plate 1), flower size, and maturation time in the growth chamber (see section on growth cycle). *Cakile arctica* and *C. edentula* ssp. *Harperi* have fruits of the same length, but

these are morphologically quite distinct, those of the former having a smooth surface and acute beak while those of the latter are 8-ribbed and usually retuse at the apex. There is, therefore, no compelling reason to regard the Icelandic and Arctic European plants as conspecific with *C. edentula* of North America. It is quite plausible that *C. arctica* may have evolved from New World progenitors, as maintained by Pobedimova (1963). Löve and Löve (1947) concluded that the Icelandic sea rockets were probably postglacial, prehistoric immigrants via the Gulf Stream from the Atlantic Coast of North America. The plants from the two areas are similar in seed size, seed glucosinolate composition, and leaf morphology. However, for all these characters and for additional floral ones, the range of variation within *C. maritima* encompasses or approaches that of *C. arctica*. It is possible that the region inhabited by *C. arctica*, which was ice-covered during much of the Pliocene and Pleistocene (Kummel 1970; Flint 1971), was invaded by colonists from Western Europe after the last glacial maximum. The existing evidence does not strongly favor one hemisphere over the other in a choice of the progenitor of *C. arctica*. My bias for an Old World ancestor is predicated upon the knowledge that the Icelandic flora, which is primarily a recently reconstituted one following glacial destruction, derives predominantly from European sources (Löve & Löve 1956).

Polunin (1959) and Hadač (1960, 1963) reported *Cakile maritima* in Spitsbergen, both reports being explicitly based on immature specimens. It is likely and, indeed, more congruent with geographical considerations that the specimens they studied were of *C. arctica*. Whether a native component of the strand flora of Spitsbergen or only a sporadic migrant to these arctic islands is not known.

7. **Cakile constricta** Rodman sp. nov.

PLATE 1; MAP 5.

Herbae annuae carnosae erectae, 1–3 dm altae, vel prostratae plerumque, ramosissimae; folia carnosa; folia prima ovata petiolata vel obovata aut spathulata et attenuata basi, lobata crenate sinuate vel dentate, pinnatifida nunquam, ad 3 × 10 cm; folia serotiniora parviora oblanceolata ± integra; racemi floriferi subcorymbiformes; racemi fructiferi lineares 1–4 dm longi, geniculati nunquam, fructibus congestis plerumque; pedicelli divergentes 2.5–7 mm longi, ca. 1 mm lati; sepala ca. 4 mm longa, 1.5–2.5 mm lata, bigibbosa basi lanceolata trichomatibus sparsis simplicibus ad apicem saepe, apice subdilatata; petala ± unguiculata 5.3–8 mm longa, 1.3–2.6 mm lata, alba vel lavandula; nectaria parva; stamina tetradynama antheris 1.0–1.4 mm longis introrsis; pistillum lanceolatum; stigma capitatum hemisphaericum vel bilobum; siliculae suberosae lanceolatae 14–22 mm longae, 3–4 mm latae, constrictae ad locum articuli; articulus inferior 5–8.5 mm longus cylindricus vel tetragonus leviter apice ± plano labio exiguo et 2 dentibus parvis plerumque; articulus superior 9–15 mm longus, ± fusiformis, teris vel tetragonus plerumque apice acuto et labio basali exiguo; semina oblonga dimorpha cotyledonibus accumbentibus.

Holotype: Florida, Bay Co., St. Andrews, 2–V–1901, *Tracy 7303* (US); isotypes: BM,F,MO,NY. CHROMOSOME NUMBER: $2n=18$ (Plate 3).

DISTRIBUTION: Atlantic Coast of Florida and shores of the Gulf of Mexico from south-central Florida to easternmost Texas. Flowering from February to October.

REPRESENTATIVE SPECIMENS. **U.S.A. Alabama: Baldwin Co.,** Perdido Bay, 18–VI–1893, *Mohr 6* (F,NY); **Mobile Co.,** without locality, 24–VI–1879, *Mohr s.n.* (US). **Florida: Brevard Co.,** Satellite Beach, 6–VI–1964, *Lakela 27206* (FLAS,GH,SMU,USF); **Escambia Co.,** Pensacola Beach, 23–IV–1941, *Fassett s.n.* (WIS); **Flagler Co.,** Flagler Beach, 10–IV–1940, *West & Arnold s.n.* (FLAS); **Franklin Co.,** Alligator Point, 13–VI–1955, *Ford & West s.n.* (FLAS,GH); **Gulf Co.,** 4.2 miles E. of Ward Ridge, 22–IV–1966, *Wooten 221* (FSU); **Indian River Co.,** Indian River, 1874, *Palmer 13* (F,GH,MO); **Levy Co.,** Seahorse Key, 12–III–1965, *Wiggins 19437* (DS,FLAS,FSU,USF); **Okaloosa Co.,** Santa Rosa Island, 9–VII–1964, *McDaniel 4908* (FSU); **Pinellas Co.,** Mullet Key, 13–IX–1963, *Thorne 33904* (RSA); **Sarasota Co.,** Sarasota Bay, 24–II–1943, *Perkins s.n.* (GH,USF); **St. Johns Co.,** Marineland, 7–II–1939, *Murrill s.n.* (FLAS,MO); **St. Lucie Co.,** Fort Pierce, 13–V–1951, *Brass 21236* (GH); **Volusia Co.,** New Smyrna Beach, 2–VIII–1970, *Lakela 32066* (GH); **Wakulla Co.,** Mashes Island, 24–IV–1955, *Godfrey 53206* (DUKE,FSU,GH,NY,USF). **Louisiana:** St. Bernard Parish, Chandeleur Island, 12–III–1959, *Lemaire 901* (FSU,LAF,US). **Mississippi: Harrison Co.,** Ship Island, 15–VI–1952, *Demaree 31925* (FSU,GA,GH,NCU); **Jackson Co.,** Petit Bois Island, 7–VIII–1952, *Demaree 32610* (DUKE,GH,LAF,RSA,SMU,WIS). **Texas: Brazoria Co.,** strand ca. 4 miles W. of San Luis Pass Bridge, 9–VII–1969, *Rodman 64* (GH).

Plants of *Cakile constricta* usually have been identified with *C. Chapmanii*, a name which, as here lectotypified, is synonymous with the distinct *C. lanceolata* ssp. *fusiformis*. *Cakile constricta* is intermediate between *C. edentula* to the north and *C. lanceolata* to the south for a number of features: fleshiness of leaves and stems, infructescence length, flower size, and spontaneous fruit set. Since it is geographically intermediate as well, it represents a probable bridge connecting the two better known American species and exemplifies some of the morphologically intermediate characters which any transitional form between *C. edentula* and *C. lanceolata* must have possessed. The occurrence of this geographic intermediate with morphologically intermediate features supports the concept of a single phyletic unit in the New World, probably derived from a single Old World introduction.

Cakile constricta is distributed disjunctly on the Atlantic Coast of Florida and on beaches of the Gulf of Mexico, being absent from southernmost, tropical Florida. This disjunction may have developed in response to the emergence of the Florida Peninsula after the last glacial maximum. The coalescence of the Pleistocene islands and emergence of a peninsula jutting southward into subtropical latitudes may have disrupted a more continuous, northern distribution. An approximation of this pattern of disjunction occurs in the genus *Verbesina*, where the closely related *V. heterophylla* in northeastern Florida and *V. Chapmanii* of northwestern coastal counties of Florida are disjunct by 150 miles (Coleman 1972).

EXCLUDED NAMES

Cakile aegyptia (L.) Sprengel, non Willd., Syst. Veg. 2: 852. 1825.=*Didesmus aegyptius* (L.) Desv.

Cakile bipinnata (Desf.) Sprengel, Syst. Veg. 2: 852. 1825.=*Didesmus bipinnatus* (Desf.) DC.

Cakile clavata (Poir.) Sprengel, Syst. Veg. 2: 852. 1825.=*Rapistrum rugosum* (L.) Allioni.

Cakile myagroides (L.) Poir., Ency. Bot. Suppl. 2: 88. 1811.=*Erucaria hispanica* (L.) Druce.

APPENDIX I. FIELD COLLECTIONS OF CAKILE ANALYZED FOR GLUCOSINOLATES (VOUCHERS IN GH).*

Number	Locality and date	Identity
24	Florida, Duval Co., sandy beach, summer 1968; seeds collected by C. E. Wood, Jr.	*C. edentula* ssp. *Harperi*
25	Texas, Galveston Co., Galveston, 25 March 1966; voucher: *Rüdenberg s.n.*	*C. geniculata*
26	Massachusetts, Barnstable Co., Sandy Neck Beach, 12 October 1968.	*C. edentula* var. *edentula*
27	Canada: Quebec, Baie St. Paul, 4 September 1964; seeds collected by R.V.D. Hende.	*C. edentula* var. *lacustris*
28	Canada: British Columbia, Vancouver Island, Oyster Bay, 6 September 1967; seeds collected by I. J. Bassett and F. J. Beales.	*C. edentula* var. *edentula*
29	Norway: Buskerud Co., Tofte, Hurumlandet, 4 October 1968; seeds collected by T. Gjelsås.	*C. maritima* ssp. *baltica*
30	Puerto Rico: sandy beach near lighthouse, NE corner of island, February 1969; seeds collected by R. A. Howard.	*C. lanceolata* ssp. *lanceolata*
31	Canada: Nova Scotia, beach at South Cove, Joggins, 13 September 1971; voucher: *Barrington 388.*	*C. edentula* var. *edentula*
32	Bahamas: Great Abaco Island, Bay Square, Crossing Rocks, 10 April 1969; seeds sent by R. O. Belcher.	*C. lanceolata* ssp. *lanceolata*
33	Bahamas: Gorda Cay, W. of Great Abaco Island, 11 April 1969; seeds sent by R. O. Belcher.	*C. lanceolata* ssp. *lanceolata*
34	Massachusetts, Essex Co., sandy beach near Beverly, 17 October 1968; seeds collected by L. Rüdenberg.	*C. edentula* var. *edentula*
39	North Carolina, Dare Co., Bodie Island, Oregon Inlet Campsite of Cape Hatteras National Seashore, 8 June 1969.	*C. edentula* var. *edentula*
40	North Carolina, Dare Co., Pea Island National Wildlife Refuge, 9 June 1969.	*C. edentula* ssp. *Harperi*
41	North Carolina, Hyde Co., Ocracoke Island, 10 June 1969.	*C. edentula* ssp. *Harperi*
43	South Carolina, Horry Co., Myrtle Beach State Park, 12 June 1969.	*C. edentula* ssp. *Harperi*
44	South Carolina, Charleston Co., Edisto Beach State Park, 12 June 1969.	*C. edentula* ssp. *Harperi*
45	Georgia, Glynn Co., Jekyll Island, 13 June 1969.	*C. edentula* ssp. *Harperi*
47	Florida, Flagler Co., Flagler Beach State Park, 16 June 1969.	*C. edentula* ssp. *Harperi*
48	Florida, Volusia Co., 1 mile south of Turtle Mound Historic Memorial, 17 June 1969.	*C. edentula* ssp. *Harperi*
49	Florida, Brevard Co., strand north of Satellite Beach city limits, 18 June 1969.	*C. constricta*
50	Florida, Brevard Co., strand about 8 miles north of Sebastian Inlet Bridge, 19 June 1969.	*C. constricta*
51	Florida, Dade Co., south end of Key Biscayne, 20 June 1969.	*C. lanceolata* ssp. *fusiformis*

Number	Locality and date	Identity
52	Florida, Dade Co., Virginia Key, Outlaw Beach, 21 June 1969.	*C. lanceolata* ssp. *fusiformis*
53	Florida, Monroe Co., strand at SW. corner of Boca Chica Key, 25 June 1969.	*C. lanceolata* ssp. *fusiformis*
55	Florida, Monroe Co., Lower Matecumbe Key at mile marker 75, 26 June 1969.	*C. lanceolata* ssp. *fusiformis*
56	Florida, Lee Co., Estero Island just N. of bridge over Big Carlos Pass, 27 June 1969.	*C. lanceolata* ssp. *fusiformis*
57	Florida, Pinellas Co., Mullet Key, Fort Desoto State Park, 28 June 1969.	*C. lanceolata* ssp. *pseudo-constricta*
58	Florida, Franklin Co., strand from Alligator Point to Bald Point, 1 July 1969.	*C. constricta*
60	Florida, Santa Rosa Co., Fort Pickens State Park, 4 July 1969.	*C. constricta*
62	Louisiana, Jefferson Parish, strand near E. end of Grand Isle, 6 July 1969.	*C. constricta* & *C. geniculata*
63	Louisiana, Cameron Parish, strand ca. 6.4 miles W. of Holly Beach, 8 July 1969.	*C. geniculata*
64	Texas, Brazoria Co., strand ca. 4 miles W. of San Luis Pass Bridge, 9 July 1969.	*C. constricta* & *C. geniculata*
65	Texas, Aransas Co., Mustang Island, strand at end of Access Road #1, 10 July 1969.	*C. geniculata* (a) & *C. lanceolata* ssp. *pseudoconstricta* (b)
66	Texas, Aransas Co., Mustang Island, strand at end of Access Road #2, 10 July 1969.	*C. geniculata*
67	Texas, Willacy Co., Port Mansfield, 11 July 1969.	*C. lanceolata* ssp. *pseudo-constricta*
69	Mexico: Baja California, Ensenada, 19 July 1969.	*C. maritima* ssp. *maritima*
71	California, Ventura Co., Point Mugu Recreation Area, 24 July 1969.	*C. maritima* ssp. *maritima*
73	California, San Luis Obispo Co., Pismo Beach State Park, 27 July 1969.	*C. maritima* ssp. *maritima*
76	California, Santa Cruz Co., Sunset Beach State Park, 29 July 1969.	*C. maritima* ssp. *maritima*
79	California, Mendocino Co., Manchester Beach State Park, 5 August 1969.	*C. maritima* ssp. *maritima*
82	California, Humboldt Co., south spit of Humboldt Bay, 8 August 1969.	*C. maritima* ssp. *maritima*
87	Oregon, Tillamook Co., strand of spit along Netarts Bay, 13 August 1969.	*C. maritima* ssp. *maritima*
89	Washington, Grays Harbor Co., strand of Twin Harbors State Park, 15 August 1969.	*C. edentula* var. *edentula*
90	Washington, Clallam Co., strand of Mukkaw Bay, 17 August 1969.	*C. maritima* ssp. *maritima*
91	Washington, Island Co., West Beach of Deception Pass State Park, 18 August 1969.	*C. edentula* var. *edentula*
94	Oregon, Clatsop Co., strand ca. 5 miles N. of Gearhart, 31 August 1969; seeds collected by C. E. Wood, Jr.	*C. edentula* var. *edentula* (a) & *C. maritima* ssp. *maritima* (b)
95	Massachusetts, Barnstable Co., Sandy Neck Beach, 28 September 1969.	*C. edentula* var. *edentula*

Number	Locality and date	Identity
96	Maryland, Worcester Co., between Ocean City and Delaware state line, 28 September 1969; seeds collected by D. Hull.	*C. edentula* var. *edentula*
97	Delaware, Sussex Co., North Bethany Beach, 28 September 1969; seeds collected by D. Hull.	*C. edentula* var. *edentula*
98	Delaware, Sussex Co., Broadkill Beach, 28 September 1969; seeds collected by D. Hull.	*C. edentula* var. *edentula*
99	Delaware, Sussex Co., Fenwick Island Beach, 28 September 1969; seeds collected by D. Hull.	*C. edentula* var. *edentula*
100	Delaware, Kent Co., South Bowers Beach, 28 September 1969; seeds collected by D. Hull.	*C. edentula* var. *edentula*
102	Indiana, Porter Co., Indiana Dunes State Park, 11 October 1969; seeds collected by D. Niemann.	*C. edentula* var. *lacustris*
103	New Hampshire, Rockingham Co., ca. 1 mile N. of Wallis Sands State Park, 18 October 1969.	*C. edentula* var. *edentula*
104	Massachusetts, Essex Co., East Point, Nahant, 19 October 1969.	*C. edentula* var. *edentula*
107	Iceland: Seltjarnarnes peninsula near Reykjavik, 29 November 1969; seeds collected by E. Einarsson.	*C. arctica*
112	Jamaica: St. Thomas Parish, strand of Holland Bay, 15 July 1970.	*C. lanceolata* ssp. *lanceolata*
114	Jamaica: St. Mary Parish, strand of Annotto Bay, 15 July 1970.	*C. lanceolata* ssp. *lanceolata*
116	Jamaica: St. Ann Parish, near Runaway Bay, 18 July 1970.	*C. lanceolata* ssp. *lanceolata*
117	Jamaica: Trelawny Parish, strand on Rio Bueno Harbor, 18 July 1970.	*C. lanceolata* ssp. *lanceolata*
118	Jamaica: Trelawny Parish, Barood Beach near Duncans, 18 July 1970.	*C. lanceolata* ssp. *lanceolata*
119	Jamaica: Trelawny Parish, Half Moon Beach near Falmouth, 18 July 1970.	*C. lanceolata* ssp. *lanceolata*
127	Bermuda: Warwick Parish, Warwick Long Bay strand, 31 July 1970.	*C. lanceolata* ssp. *lanceolata*
128	Bermuda: Paget Parish, strand of Grape Bay, 1 August 1970.	*C. lanceolata* ssp. *lanceolata*
129	Mexico: Veracruz, sandy beach N. of Nautla, June 1970; seeds collected by L. Nevling (voucher: *Nevling & Gomez-Pompa 1258*).	*C. geniculata*
130	Florida, Charlotte Co., Englewood Beach, 25 July 1970; seeds sent by O. Lakela.	*C. lanceolata* ssp. *fusiformis*
131	Florida, Volusia Co., New Smyrna Beach, 2 August 1970; seeds collected by O. Lakela.	*C. edentula* ssp. *Harperi*
132	Michigan, Berrien Co., Warren Dunes State Park, 31 August 1970.	*C. edentula* var. *lacustris*
133	Michigan, Allegan Co., Holland State Park, 31 August 1970.	*C. edentula* var. *lacustris*

Number	Locality and date	Identity
136	Maine, Popham Beach State Park, 7 October 1970.	*C. edentula* var. *edentula*
137	Maine, Mt. Desert Island, Acadia National Park, 8 October 1970.	*C. edentula* var. *edentula*
150	Massachusetts, Nauset Beach, Cape Cod, 12 October 1968.	*C. edentula* var. *edentula*
151	Massachusetts, Race Point Beach, Cape Cod, 12 October 1968.	*C. edentula* var. *edentula*
152	Denmark: Jutland peninsula near Hansted on the North Sea, 1972; seeds sent by M. Ettlinger.	*C. maritima* ssp. *maritima*
153	Denmark: Sjaelland Island, Staengehuse, 1972; seeds sent by M. Ettlinger.	*C. maritima* ssp. *baltica*
154	Denmark: Ise Fiord, Kulhuse, 1972; seeds sent by M. Ettlinger.	*C. maritima* ssp. *baltica*
B–103	Bahamas: Great Abaco Island, coastal dunes ½ miles S. of Crossing Rocks, 5 February 1969; collected by R. O. Belcher.	*C. lanceolata* ssp. *lanceolata*
F–41920	Mexico: Alacran Islands, Desterrado Islet, 5 July 1961; voucher: *Fosberg 41920* (US).	*C. lanceolata* ssp. *alacranensis*
G–7659	Florida, Dade Co., Cape Florida State Park, 15 March 1969; voucher: *Gillis 7659*.	*C. lanceolata* ssp. *fusiformis*
P–*s.n.*	Australia: Victoria, Black Rock strand, 7 December 1971; voucher: *Parsons s.n.*	*C. maritima* ssp. *maritima*
R–*s.n.*	Virgin Islands: St. John Island, strand of Trunk Bay, 11 September 1968; seeds collected by C. E. Wood, Jr.; voucher: *Rollins s.n.* (greenhouse plant).	*C. lanceolata* ssp. *lanceolata*
W–9138	Florida, Monroe Co., Big Pine Key, April 1966; voucher: *Wood 9138*.	*C. lanceolata* ssp. *fusiformis*

*Vouchers not otherwise designated collected by the author.

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REVISIONS OF SOME GENERA OF CRUCIFERAE NATIVE TO AUSTRALIA

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In a series of revisional studies (Shaw 1965, 1970, 1972) I have provided treatments of the genera of Cruciferae which are endemic to Australia. In Australia there are, in addition to the endemic genera, species, both native and introduced, of *Lepidium*, *Cardamine*, *Rorippa*, and *Nasturtium*. Australia has also a full complement of common weedy species of genera such as *Brassica*, *Sinapis*, *Diplotaxis*, *Coronopus*, and *Sisymbrium*, two species of *Cakile* and, in Western Australia, the South African species *Heliophila pusilla*. None of these has been involved, either taxonomically or nomenclaturally, in the difficulties associated with determination of the generic disposition of the species in the endemic genera and I have made no study of them. Leaving aside these genera, as well as *Menkea* (Shaw, 1970), *Stenopetalum* (Shaw, 1972), and *Blennodia*—in the sense of Flora Australiensis (see Shaw, 1965)—there remain fifteen species, although rather more than fifteen names, to be considered.

Two of these species, although not commonly weedy, are certainly introduced. Plants indistinguishable from those in European populations of *Hymenolobus procumbens* (L.) Nutt. ex Schinz & Thell. are common in coastal districts in southern Australia. A species now common in arid areas of South Australia is *Alyssum linifolium* Steph. ex Willd. of southern Europe and the Middle East. Collections of this species were made by Mueller in both Western Australia and South Australia not many years after the colonies were established; for example, in 1850 at Kanyaka, north of Port Augusta, then far beyond the settled areas. However John Eyre with his exploring party had been in the area as early as 1839, and introduction of this species was quite possible. Four other species are easily accounted for. *Cheesmannia radicata* (Hook. f.) Schulz is the endemic Tasmanian representative of a genus otherwise restricted to New Zealand and is not closely related to any of the Cruciferae of the Australian mainland. *Thlaspi tasmanicum* (Hook.) Hook. f. still is known only from the original collection made in 1848 at Arthur's Lake in central Tasmania. *Draba pumilio* R. Br. ex DC., possibly conspecific with *Ballantinia antipoda* (F. Muell.) E. Shaw, was also described from Tasmanian plants; it, too, is known only from a single collection and the name is based on plants too immature to be referred with certainty to a genus. *Carinavalva glauca* Ising, the sole species of the genus, seems to occur only in a restricted area to the south and southwest of Oodnadatta in South Australia. The plants are glaucous annuals with deeply pinnatisect leaves, long narrow petals much like those of *Stenopetalum*, and strongly obcompressed siliques containing numerous ovules.

The remaining nine species, all endemic, have little in common as a group, save that several were first described as species of *Capsella* or of *Hutchinsia*, were subsequently juggled by various authors among *Capsella*, *Thlaspi*, and *Hutchinsia*, and finally were transferred by Schulz (1933, 1936) to one of his newly described genera. However, *Capsella and Hutchinsia* are essentially European and I believe that inclusion of the Australian species in such genera stretches to an uncomfortable degree both the morphological and geographical boundaries of the European genera. *Capsella* of all modern authors includes the now widely spread ruderal species, *C. bursapastoris*, and four or five similar species which occur accross Europe into the USSR. These plants are annuals or biennials with stems arising from a basal rosette of leaves, and all have emplexicaul leaves and loose infructescences of obcordate siliques. In Flora Europaea, Heywood and Jones (1964) include in the genus *Hutchinsia* only one species, *H. alpina*, a small montane perennial which has pinnatisect leaves and siliques which are elliptic to lanceolate, obcompressed and with one or two ovules in each locule. Sometimes segregated from *Hutchinsia* is *Hornungia* to which Heywood referred two species, *H. aragonensis* from the mountains of northeastern Spain, and *H. petraea*, a montane calciphile widespread in central Europe. The plants are annuals, glabrous or with stellate trichomes, but otherwise much like *Hutchinsia*. Related to these species is *Hymenolobus procumbens* (L.) Nutt. ex Schinz & Thell. (*Hutchinsia procumbens* (L) Desv.; *Hornungia procumbens* (L.) Hayek), a widely and disjunctly spread species of halophytic tendencies known from Europe, northern Africa, central Asia, North America, Chile, and Australia. This is a rather variable species which differs from *Hornungia petraea* by more numerous ovules and simple, rather than stellate, trichomes. Often the basal leaves are entire, and the siliques, which are truncate or emarginate, have thin-walled valves which are translucent. *Thlaspi*, which differs most markedly from *Capsella* by the winged siliques of the species of the former genus, covers a greater geographical range than does either *Hutchinsia* or *Hornungia*, but most of the sixty-odd species of *Thlaspi* are in Europe and central Asia, the others in North and South America. It may be, however, that the species described by Hooker from central Tasmania is indeed a *Thlaspi*; if so, it is the only one native to Australia.

The last general treatment of the family was prepared by O. E. Schulz (1936). When Schulz dealt with the Australian species he had as a foundation for study Bentham's (1863) treatment of the family for Flora Australiensis and a few species described over the following fifty years by Ralph Tate or J. M. Black. Bentham had erred as a lumper in his circumscription of *Blennodia*. His treatments of *Menkea* and of *Stenopetalum* were satisfactory for the time, but the miscellany of species here dealt with, he distributed between *Capsella* and *Hutchinsia*. On the whole, Schulz' famed propensity for splitting led him astray among the

Australian Cruciferae in a way much less marked than it did, for example, among those of the western part of North America. Schulz responded to the challenge of the Australian Cruciferae by describing nine new genera, seven of these—a few too many (Shaw, 1965)—in the tribe Sisymbrieae, and two, *Phlegmatospermum* and *Cuphonotus*, in the tribe Lepidieae. Although his referral of species to the two latter genera was erratic, the concept is sound, and six of the group of nine species here dealt with belong to one or the other of these genera. *Phlegmatospermum*, as I understand the genus, includes four species which have siliques strongly obcompressed and keeled, and flowers with unguiculate and comparatively large petals. In *Cuphonotus* I include two species in which the siliques, although obcompressed, have the valves dorsally rounded and the small flowers have linear or obovate petals. Although Schulz placed these genera into different subtribes of the Lepidieae, I believe them to be closely related.

The two species here referred to *Microlepidium* have winged siliques, the seminiferous parts of which are, in fact, very little compressed. *Microlepidium alatum*, described in 1937, was not known to Schulz, and *M. pilosulum* he retained, with some doubt, in *Capsell*a where Mueller had placed it. Resemblances between this species and those of *Capsella* are only superficial. Although the siliques of both species of *Microlepidium* can be described as obcordate, much of each fruit is solid tissue and the seeds are both few in number and small in size as compared to those of *Capsella*. The flowers of both species of *Microlepidium* are very small with widely spreading sepals, and those of *M. alatum* seem always to be apetalous.

The last of the nine species has been twice described, by Ferdinand von Mueller as *Capsella antipoda*, and by J. D. Hooker as *Hutchinsia australis*, and it has been transferred under both names to *Cuphonotus*. Apart from other considerations, this species differs from species of *Capsella* and of *Hutchinsia* in fruit structure, and from *Cuphonotus*, very markedly so, in both flowers and fruit. I can find, in fact, no evidence to indicate that it is closely related to any others of the Australian genera. Hooker himself suspected that his *Hutchinsia australis* was best treated as representing a distinct genus. I agree with Hooker's view and here describe the genus *Ballantinia* including the single species, *B. antipoda* (F. Muell.) E. Shaw.

ACKNOWLEDGEMENTS

I wish to thank Mrs. Lily Rüdenberg for her patience in dealing with refractory cytological material and Mrs. Maria Szent-Ivany of Adelaide for her preparation of the illustrations. I am grateful also to the curators of the herbaria housing those specimens studied; the herbaria are cited by the standard abbreviations of Lanjouw and Stafleu (Regnum Veg. 31: 1964).

1. **Phlegmatospermum** O. E. Schulz, Bot. Jahrb. 66:93. 1933.

Plants pubescent annuals, the stems erect or spreading; basal leaves usually pinnatisect; cauline leaves usually shallowly dentate or sinuate; sepals spreading and often persistent, not saccate; petals white, creamy, or yellow, unguiculate; ovules 3–10 in each locule; siliques elliptic or obovate to suborbicular, strongly obcompressed and angustisept, sometimes notched; style short, the stigma as wide as the style; seeds oblong to ellipsoid, not flattened, the testa copiously mucose when moistened; cotyledons incumbent or obliquely so. Lectotype species: *Phlegmatospermum cochlearinum* (F. Muell.) O. E. Schulz.

EXCLUDED SPECIES: *Phlegmatospermum Andraeanum* (F. Muell.) O. E. Schulz=*Cuphonotus Andraeanus* (F. Muell.) E. Shaw; *Phlegmatospermum villosulum* (F. Muell. ex Tate) O. E. Schulz=*Menkea villosula* F. Muell. ex Tate.

KEY TO THE SPECIES OF PHLEGMATOSPERMUM

Trichomes with rays closely appressed, 2-rayed and sessile or subsessile. Plants usually erect; petals 3–7 mm. long; siliques elliptic to suborbicular, 6–13 mm. long, not notched. . . . . 1. *P. cochlearinum.*

Plants usually prostrate and spreading; petals 2–3 mm. long; siliques elliptic probably less than 10 mm. long. . . . . 2. *P. eremaeum.*

Trichomes with rays ascending and not appressed, 2- to 4-rayed, sessile or on a short but distinct base.

Trichomes distinctly stipitate and sometimes 3- or 4-rayed; only in Western Australia. . . . . 3. *P. Drummondii.*

Trichomes subsessile, but the rays erect or at least curved upwards; known only from the coast of South Australia between Eucla & Fowler's Bay. . . . . 4. *P. Richardsii.*

1. **Phlegmatospermum cochlearinum** (F. Muell.) O. E. Schulz

Map 1

Phlegmatospermum cochlearinum (F. Muell.) O. E. Schulz, Bot. Jahrb. 66:93. 1933.

Eunomia cochlearina F. Muell., Linnaea 25:369. 1853. Lectotype: South Australia. Interflumina Broughton & Rocky-creek, F. Mueller. 1851 (MEL 7696).

Thlaspi cochlearinum (F. Muell.) F. Muell., Plants Indig. Colony Victoria 1:51. 1862.

Capsella cochlearina (F. Muell.) F. Muell., Fragm. Phytog. Austral. 11:26. 1878.

Hutchinsia cochlearina (F. Muel.) J. M. Black, Flora South Austral. 254. 1924.

Thlaspi ochranthum F. Muell. ex Bentham, Flora Austral. 1:88. 1863. Lectotype: New South Wales. Upper Darling tributaries. *Bowman* (MEL 10982).

Capsella ochrantha (F. Muell. ex Benth.) F. Muell., Fragm. Phytolg. Austral. 11:26. 1878.

C. cochlearina var. *ochrantha* (F. Muell. ex Benth.) Maiden & Betche, Census N.S. Wales Pl. 84. 1916.

Hutchinsia ochrantha (F. Muell. ex Benth.) J. M. Black, Flora South Austral. 254. 1924.

Phlegmatospermum ochranthum (F. Muell. ex Benth.) O. E. Schulz, Bot. Jahrb. 66:93. 1933.

P. cochlearinum var. *ochranthum* (F. Muell. ex Benth.) J. M. Black, Trans. Roy. Soc. S. Austral. 61:245. 1937.

Plants erect annuals, pubescent; trichomes malpighiaceous; stems to 2.5 dm. long, sometimes much branched; basal leaves rosulate, 9 cm. long and 2 cm. wide, elliptic to narrowly obovate, coarsely dentate or entire; cauline leaves to 6 (9) cm. long and 1 (2) cm. broad, obovate to elliptic, entire or remotely dentate; inflorescences dense but

rapidly elongating after anthesis, buds round to ellipsoid; sepals 2–4 mm. long, elliptic to obovate, not saccate but usually cucullate; petals 3–7 mm. long, white or yellow, unguiculate, the blade usually orbicular and narrowed to the linear claw; stamens 2–6 mm. long, the filaments expanded at the base; glandular tissue square to hexagonal around the single stamens, usually absent between the paired stamens; ovules 4–10 in each locule; infructescences loose; pedicels to 2.5 cm. long, rather stout and spreading; siliques 6–13 mm. long, round to elliptic and strongly obcompressed, the valves glabrous on the interior, pubescent on the exterior, the trichomes parallel to the long axis of the fruit; styles 1–2.5 mm. long, the stigmas capitate and epressed; septum entire; seeds 1.5–2.5 mm. long, ellipsoid, red- or orange-brown, papillose. $n=6$ (plants from seed of *Shaw 510*).

DISTRIBUTION: From central New South Wales across South Australia into the eastern part of Western Australia.

REPRESENTATIVE SPECIMENS: **New South Wales.** Dubbo, *Boorman*, 1903 (NSW *77584*); Hillston, *Evans*, 1889 (MEL *11013*); Bourke, *Constable*, 1947 (NSW *4611*); 50 miles east of Wilcannia, *Burbidge*, 1960 (CANB,NSW 77583); Wilcannia, *Beadle*, 1939 (SYD); Menindee, *Constable*, 1955 (NSW 39939); near Poole's Grave, *Morris* 826 (AD,ADW,NSW *77588*—syntype of *Hutchinsia eremaea* Black); Fowler's Gap, *Dinning*, 1955 (NE). **South Australia.** Lake Harry, *Hill 300* (AD); 3 km. east of Ediacara, *Lothian 2436* (AD); 16 km. northwest of Teetulpa, *Donner 357* (AD); Muloorina Homestead, *Hill 161* (AD); Hookina, *Tate*, 1883 (AD); Arkaringa Creek, *Helms*, 1891 (AD,K,MEL *10979, 10980*, NSW *77580*); Yudnapinna, *Hilton 671* (ADW); Hughes, *Ising*, 1920 (AD,MEL *7691, 7692*, NSW *77575*—syntype of *Hutchinsia eremaea* Black); Nullarbor Plain (between White Wells and Cook), *Hilton*, 1955 (ADW). **Western Australia.** 3 miles south of Reid, *Aplin*, 1961 (PERTH); 14 miles east of Forrest, *Aplin 1665* (PERTH). **Queensland.** Silverwood, *White*, 1922 (BRI).

Although this is the most widely spread species of *Phlegmatospermum* it is nowhere abundant and seems never to have been common. Mueller (1862) referred to it as "an equally [to *Thlaspi tasmanicum*] rare South Australian species" and in 1878 (Fragm. Phytog. Austral. 11:26) remarked, "*Capsella cochlearina* . . . post annos triginta non iterum detecta est, ... "As Mueller himself realized, *Thlaspi ochranthum*, in floristic works often maintained as a separate species, or as a variety of *P. cochlearinum*, is only a yellow-flowered form of this species. It is sometimes said that the yellow-flowered plants are smaller than "typical" *P. cochlearinum*, but this a point taken from the protologue of *T. ochranthum*, a name based on depauperate plants of this species.

2. **Phlegmatospermum eremaeum** (J. M. Black) E. Shaw, comb. nov.

MAP 2

Hutchinsia eremaea J. M. Black, Trans. Roy. Soc. S. Austral. 47:369. 1923. Lectotype: South Australia. Exact locality unknown, Tate ? (AD); probable isolectotype (MEL *10970*). This sheet is labelled "R. Murray at Morgan, R. Tate, Sept. '83."

Phlegmatospermum cochlearinum var. *eremaeum* (J. M. Black) J. M. Black. Trans. Roy. Soc. S. Austral. 61:245. 1937.

Plants usually prostrate and spreading, more rarely erect, pubescent; trichomes sessile or shortly stipitate, biramous, the rays appressed; stems slender, 2–10 (20) cm. long; basal leaves rosulate, to ca. 4 cm. long, usually pinnatisect, sometimes only sinuate

or, especially on small plants, entire; cauline leaves to 2 cm. long, obovate, usually coarsely dentate; inflorescences dense, buds ellipsoid; sepals 1.5–2 mm. long, white or creamy, unguiculate, the claw linear and expanded into the round or obovate blade; stamens 1.5–2 mm. long, filaments flattened and widened toward the base; glandular tissue consisting of a deltoid lobe, one on each side of each single stamen, absent between the paired stamens; ovules 5–7 in each locule; infructescences usually dense and often nearly fasciculate, sometimes arising from basal inflorescences; pedicels to 1.5 cm. long (2 cm. in basal infructescences), erect to divaricately spreading; siliques to 7 mm. long, elliptic and strongly obcompressed, notched at the distal end; valves glabrous or sparsely pubescent on the exterior, glabrous within, keeled; styles very short, the stigmas flat and not markedly capitate; septum opaque and wrinkled; seeds 1 mm. long, ellipsoid, red- to orange-brown.

DISTRIBUTION: Known in South Australia from the Murray scrub and Wudinna on the Eyre Peninsula; in Western Australia from the Coolgardie area.

OTHER SPECIMENS SEEN: **Victoria.** Near junction of Darling and Murray River, *Minchin,* 1887 (MEL *7690*); western outskirts of Red Cliffs settlement, *Ramsey,* 1951 (MEL *7689*). **South Australia.** Morgan, *Tate,* 1883 (AD,MEL *10970*); Wudinna, *Ising,* 1938 (AD). Karoonda, *Cleland,* 1954 (AD); Mundoora Reserve, *Kraehenbuehl 1196* (AD). **Western Australia.** Coolgardie, *Helms,* 1899 (PERTH); Mt. Moore, *Merrall,* 1889 (MEL *11009*); Mulline, *Maryon,* 1916 (BM).

In the protologue of *Hutchinsia eremaea* Black cited three localities, "Murray lands; Nullarbor Plain. Also in the Grey Range, New South Wales." Material in Black's herbarium (AD) shows that "Nullarbor Plain" is based on a collection made at Hughes by E. H. Ising which is *P. cochlearinum.* The record for the Grey Range is based on *Morris 826,* also *P. cochlearinum,* collected "near Poole's Grave." James Poole, who died while with Sturt's expedition of 1844–1845, is buried near Mt. Poole, about 190 miles north of Broken Hill. The third collection, on which the Murray lands record is based, was more difficult to trace, but in Ralph Tate's herbarium (AD) was found a manila folder on which had been written by Black, "Hutchinsia eremaea, JMB." Pasted on the folder is a clipping, taken from Tate's census of the flowering plants and ferns of South Australia (Trans. Roy. Soc. S. Austral. 3:51. 1880) which identifies it as *Capsella humistrata,* the locality for which species is given in the census as "M" [= Murray lands]. As this folder bears the clipping, pasted on in Tate's own time according to Professor T. G. B. Osborn, and Black's annotation, it is certainly the collection cited in the protologue. It was, most likely, made at Morgan on the Murray River.

The plants are usually prostrate and quite small, the main stems sometimes reduced to basal inflorescences which have pedicels longer than those of normally developed stems. This species can be distinguished from *P. cochlearinum* by the trichomes, smaller flowers, and dense infructescences.

3. **Phlegmatospermum drummondii** (Benth.) O. E. Schulz

MAP 1

Phlegmatospermum drummondii (Benth.) O. E. Schulz, Bot. Jahrb. 66:93. 1933.
Thlaspi Drummondii Bentham, Flora Austral. 1:88. 1863. Holotype: Western Australia. "1845. Suppl. Drummond, Swan R. 4" (K), probable isotype (MEL *10977*).
Capsella Drummondii (Benth.) F. Muell., Fragm. Phytog. Austral. 11:26. 1878.
Hutchinsia Drummondii (Benth.) J. M. Black, Flora South Austral. 254. 1924.

Plants erect annuals, pubescent; trichomes on a short but distinct stalk, predominantly two-rayed, occasionally 3- or 4-rayed, the rays spreading and not appressed; stems to 3 dm. long; basal leaves rosulate, to 3.5 cm. long, pinnatisect or sinuate, usually withered and lost on older plants; cauline leaves usually less than 1 cm long, the lower leaves pinnatisect, the upper sinuate or lobed; inflorescences initially dense, but soon elongating, the buds small and globose; 1.5–2 mm. long, oblong to elliptic, neither saccate nor markedly cucullate; petals 2–3 mm. long, white or creamy, usually unguiculate, the linear claw gradually expanded into the obovate to round blade; stamens 1.5–2.5 mm. long, filaments often expanded at the base; glandular tissue square around the single stamens and subtending the paired stamens, thus forming a complete ring; ovules 3–6 in each locule; infructescences loose, pedicels 3–7 mm. long and stout, usually divaricately spreading; siliques 6.5–8 mm. long, obovate and strongly obcompressed, at the distal end notched by the separation of the valves from the replum; styles short and linear, the stigma small and little capitate; septum entire; mature seeds not seen.

DISTRIBUTION: Known only from Austin District in Western Australia.

OTHER SPECIMENS SEEN: **Western Australia.** Southern Cross, *Heal*, 1895 (MEL *10935*); Cunderdin, *Fitzgerald*, 1903 (NSW *77573*, *77574*), *Staer*, 1905 (E); Cowcowing, *Koch 1080a* (NSW *77572*), *Staer*, 1905 (E); Parker's Range, *Merrall*, 1890 (MEL *11010*); Lake Monger, *Koch 1323* (AD,MEL *10978*). There is also in the National Herbarium of New South Wales (NSW 53572) a mixed collection of this species and of *Menkea villosula* with two labels, one "Nannine," the other "Lamlens" (?) or "Lawlers."

This species, like *Menkea draboides* known from the same area, has not been collected for 70 years, but both are short-lived perennials and may have been overlooked by collectors.

4. **Phlegmatospermum richardsii** (F. Muell.) E. Shaw, comb. nov.

MAP 2

Erysimum Richardsii F. Muell., Fragm. Phytog. Austral. 10:105. 1877. Holotype: Western Australia. Eucla, *Richards* (MEL *771*), fragments (AD).
Sisymbrium Richardsii (F. Muell.) F. Muell., First System. Census 5. 1882.
Blennodia Richardsii (F. Muell.) J. M. Black, Flora South Austral. 247. 1924.
Scambopus Richardsii (F. Muell.) O. E. Schulz, Pflanzenreich, ed. 2, 86:260. 1924.

Plants erect annuals, pubescent; trichomes sessile or subsessile, 2-rayed, the rays spreading and slightly curved upwards; basal leaves to 7 cm. long, obovate, entire or remately lobed or dentate, on a long, slender petiole; cauline leaves to about 4 cm. long, obovate or oblanceolate, entire to shallowly lobed; inflorescences initially dense, but soon elongating, the buds ellipsoid; floral organs apparently as in *P. cochlearinum*, often persistent around the developing fruit; infructescences loose, pedicels about 1 cm. long and stout, divaricately spreading; siliques to 1 cm. long, densely pubescent on the exterior, glabrous on the exterior; styles slender, conspicuously extending beyond the valves; stigmas small and about as wide as the style; mature seeds not known.

DISTRIBUTION: Known only from the head of the Great Australian Bight.

OTHER SPECIMENS SEEN: **South Australia.** Near Fowler's Bay, anon. Richards ? (E, MEL *7694*, P); head of the Great Australia Bight, *Mrs. Richards,* 1879 (AD); between Fowler's Bay and Eucla, *Richards* (AD,MEL *10976*). **Western Australia.** Near Eucla, *Mrs. Richards,* 1879 (AD). Without locality or collector (MEL).

The synonymy of this little-known species suggests a grasping at generic straws in the effort to find its proper systematic position. The holotype is a small plant, only in flower, and all later collections seem to have been originally referred, as *Capsella Drummondii,* to the Western Australia species, *P. Drummondii.* All of the material which I have seen was collected during 1877–1880, along the Bight, by one or other of the Richards, then at the telegraph repeater station at Eucla. The collections made in 1879 and 1880 include plants, bearing young fruit, which leave no doubt that this is a *Phlegmatospermum,* distinct from both *P. Drummondii* and the more widely spread *P. cochlearinum.*

Phlegmatospermum richardsii is most easily distinguished from both of these species by the trichomes on the fruit. Those of *P. Drummondii* are 2- to 4-rayed and have a distinct stipe; the trichomes of *P. cochlearinum* are 2-rayed and appressed and those on the siliques are usually oriented parallel to the longitudinal axis, but the trichomes of *P. richardsii,* although subsessile and 2-rayed, always have the rays spreading. In the absence of evidence to the contrary, I prefer to maintain *P. richardsii* as a distinct species closely related to *P. cochlearinum.*

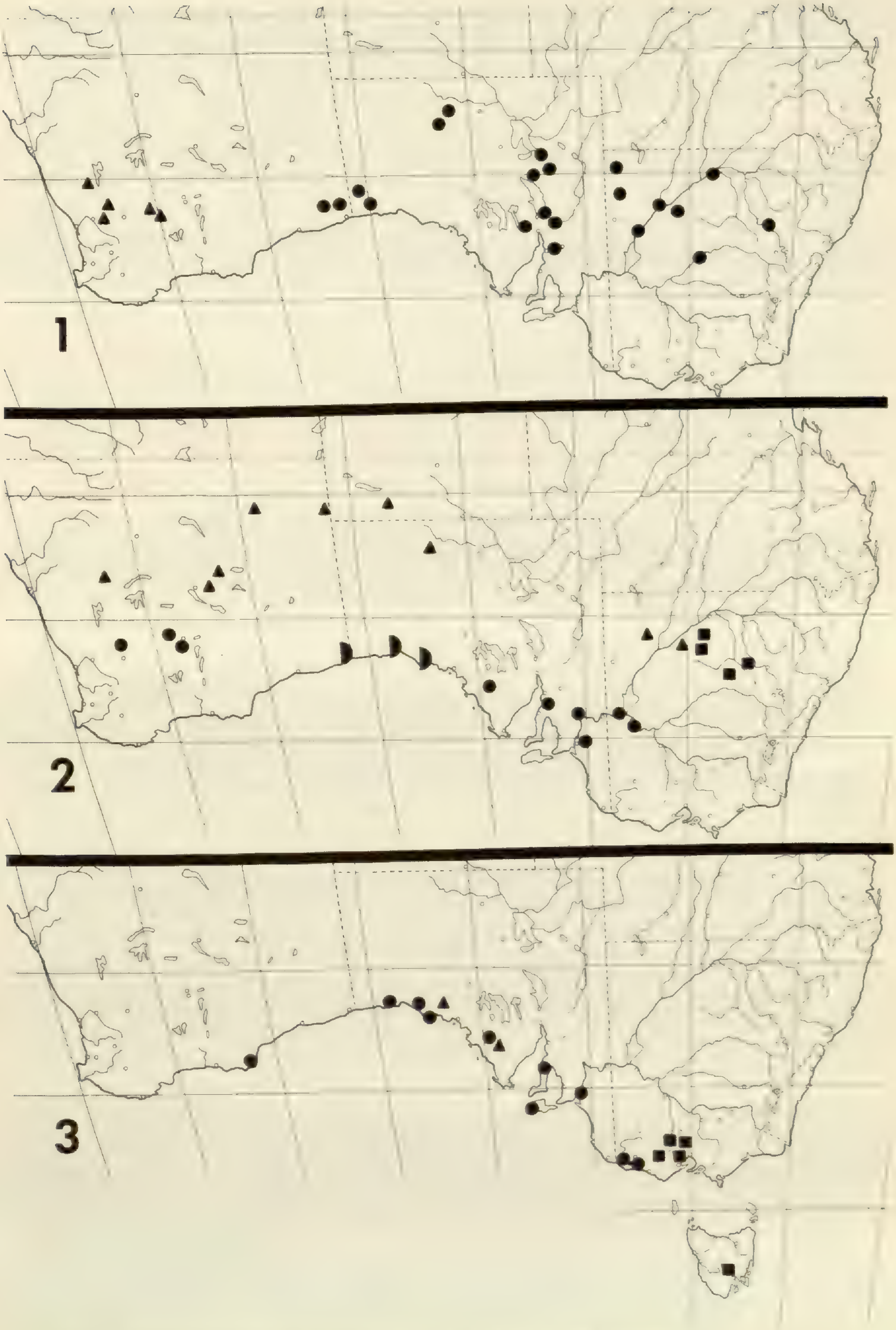
I have seen the latter species from the Nullarbor Plain, both in Western Australia and in South Australia, and there are a few collections made between the coast of South Australia and the Eyre Highway. These all have the 2-rayed, strongly appressed trichomes just mentioned. *Phlegmatospermum richardsii* seems not to have been collected since 1880, but this must be, in part, a result of the comparatively little botanical field work done in this area.

Cuphonotus O. E. Schulz, Bot. Jahrb. 66:92. 1933.

Plants glabrous or pubescent annuals, the stems erect or spreading; basal leaves entire or shallowly lobed; cauline leaves similar but smaller; sepals spreading, not saccate; petals linear or narrowly obovate, often lobed at the distal end; ovules (1) 3–7 in each locule; siliques round to broadly elliptic, obcompressed but not keeled; styles short or obsolete, the stigmas depressed-capitate or obscurely bilobed; seeds ellipsoid and flattened, mucose when moistened; cotyledons incumbent. Lectotype species: ***Cuphonotus humistratus*** (F. Muell.) O. E. Schulz.

Excluded species: *Cuphonotus australis* (Hook. f.) O. E. Schulz=*Ballantinia antipoda* (F. Muell.) E. Shaw.

Although Schulz (1936) placed *Cuphonotus* (Lepidiinae) and *Phlegmatospermum* (Capsellineae) into separate subtribes of the Lepidieae, these genera are, I believe, closely related. The greatest difference between the subtribes, as defined by Schulz, is in the embryos, the Lepidiinae described as having stipitate cotyledons, the stipe longer than



Map 1. Phlegmatospermum cochlearinum (dot); P. drummondii (triangle).

Map 2. Phlegmatospermum eremaeum (dot); P. richardsii (semi-circle); Cuphonotus humistratus (square); C. andraeanus (triangle).

Map 3. Microlepidium pilosulum (dot); M. alatum (triangle); Ballantinia antipoda (square).

the radicle, and the cotyledons usually folded in the seed. Both of the species which I refer to *Cuphonotus* do have shortly stipitate cotyledons, but they are not bent, and I find it difficult to accept this minor difference in the embryos as a valid reason for placing these genera in distinct subtribes. *Cuphonotus* differs from *Phlegmatospermum* in that the siliques do not have an apical notch, and the valves are rounded rather than keeled. The flowers of *Cuphonotus* are smaller, with narrow obovate petals which are not unguiculate, and the stamens are spreading rather than nearly erect as in *Phlegmatospermum*.

KEY TO THE SPECIES OF CUPHONOTUS

Plants glabrous; petals 2–3 mm. long; silique valves coarsely reticulate. ..... 1. *C. humistratus.*
Plants pubescent with uncinulate or curly trichomes; petals 1–1.5 mm. long; silique valves nearly smooth. ..... 2. *C. andraeanus.*

1. **Cuphonotus humistratus** (F. Muell.) O. E. Schulz

Map 2

Cuphonotus humistratus (F. Muell.) O. E. Schulz, Bot. Jahrb. 66:92. 1933.
Capsella humistrata F. Muell., Fragm. Phytog. Austral. 11:25. 1878. Lectotype: New South Wales. Near the Lachlan River, F. Mueller, 1878 (MEL *10961*); isotypes (AD,BM, K,MEL,P,W).
Hutchinsia humistrata (F. Muell.) J. M. Black, Flora South Austral. 254. 1924.

Plants spreading or erect annuals, glabrous; stems to 2.5 dm. long, often much branched; basal leaves to 3 cm. long, entire to shallowly pinnatifid, withering early and soon lost; cauline leaves to 2 cm. long, usually pinnatifid with 2 or 3 lobes per side, sometimes entire or remotely dentate; inflorescences elongate at anthesis, buds globose; sepals 1.3–2.5 mm. long, oblong to elliptic, cucullate but not saccate; petals 2–3 mm. long, apparently white, narrowly obovate and often shallowly lobed; stamens spreading, 1–2 mm. long, the filaments often bulbous at the base; glandular tissue often crescentic on each side of each single stamen and subtending the paired stamens but absent between them; ovules 1–5 in each locule; infructescences loose, the pedicels about 1 cm. long, usually divaricate, sometimes horizontal or recurved; siliques 2.5–5 mm. long, round or broadly elliptic and strongly obcompressed, the valves glabrous within and without, conspicuously reticulate; styles short or obsolete, the stigmas depressed-capitate; septum entire; seeds 1.5–2.2 mm. long, ellipsoid and flattened, brown or reddish-brown.

DISTRIBUTION: Known only from Western New South Wales, although recorded by Bailey (1899) from southern Queensland.

OTHER SPECIMENS SEEN: **New South Wales.** Cobar, *Andrae,* 1883 (MEL *10967, 11025*), *Cleland* (AD), *Cleland,* 1911 (AD), *Boorman,* 1903 (AD); Upper Darling River, *Day,* 1878 (MEL *10968*); Lachlan District, *T. Duff* (W); Trangie, *Hutchings 42* (CANB); Pulpalla, *Josephson 302* (MEL *10971*); Condobolin Flats, *Maiden,* 1897 (AD, MEL *10966*); between the Bogan and Darling's River, *Lockhart Morton,* 1877 (MEL *10972*).

The two species of *Cuphonotus* are much alike, but are easily distinguished by the unusual flattened and uncinulate trichomes and the smooth

siliques of *C. andraeanus*. *Cuphonotus humistratus* is always glabrous and the siliques, more strongly obcompressed than those of *C. andraeanus*, are roughened by conspicuously reticulate lateral veins. At the distal end the valves are abruptly contracted into a short acute beak.

Both species are arid-zone ephemerals and sometimes show extreme reduction of the stems, so that inflorescences may arise directly from the basal rosette of leaves, and these basal infructescences always have pedicels much longer than do those on normally developed stems. As is true of many other desert ephemerals, these species are often missed or ignored by collectors and *Cuphonotus humistratus* should be looked for in Queensland and South Australia.

2. **Cuphonotus andraeanus** (F. Muell.) E. Shaw, comb. nov.

Map 2

Capsella andraeana F. Muell., Wing's Southern Science Record 1 (n.s.): 49. 1885. Lectotype: New South Wales. N.W. of Cobar. Lachlan's River, *H. Andrae*, 1884 (MEL *10974*).

Phlegmatospermum Andraeanum (F. Muell.) O. E. Schulz, Bot. Jahrb. 66:93. 1933.

Cuphonotus humistratus var. *papillosus* O. E. Schulz, Bot. Jahrb. 66:92. 1933. I have seen no specimen annotated by Schulz with this name, but the description leaves no doubt as to its identity. The illustration of "Cuphonotus humistratus" (fig. 241) in Band 17b of "Die natürlichen Pflanzenfamilien" is also referable to this species.

Plants spreading or erect annuals, pubescent; trichomes simple, flattened or terete, uncinulate or twisted; stems to 2.5 dm. long, often decumbent; basal leaves to 3 cm. long, linear to spathulate and usually entire, subsucculent but withering early and soon lost; cauline leaves to 2 cm. long, as the basal leaves but smaller; inflorescences initially dense, buds subglobose; sepals 1–1.5 mm. long, elliptic to oblong and conspicuously cucullate, but not saccate; petals 1–1.5 mm. long, white to creamy or yellow, linear to narrowly obovate, sometimes irregularly lobed at the distal end; stamens spreading, 1–1.5 mm. long, the filaments often bulbous at the base; glandular tissue deltoid on each side of each single stamen and usually subtending the paired stamens, but absent between them; ovules (2)4–7 in each locule; infructescences loose, the pedicels usually about 1 cm. long, generally divaricate, rarely horizontal or recurved; siliques 2.5–5 mm. long, broadly elliptic to suborbicular and obcompressed, the valves glabrous within and without, rounded on the back and quite smooth; styles very short or obsolete, the stigmas depressed-capitate or obscurely bilobed; septum entire; seeds 1.2–1.4 mm. long, elliptic and flattened, orange-brown.

DISTRIBUTION: Widely spread across eremaean Australia, but apparently rare; found in southwestern Queensland, western New South Wales, northwestern South Australia, southern Northern Territory, eastern Western Australia.

OTHER SPEDIMENS SEEN: **Queensland.** Boatman Station, *S. L. Everist 2860* (CANB). **New South Wales.** Pulpalla, *H. Andrae 185* (MEL *10973*), *W. Woolls* (NSW *77577*), *Josephson*, 1885 (MEL *10975*); Tarella, *Bauerlen* 87 (MEL *10997*); Paroo River District, *Betche*, 1900 (BM,MEL *77576*). **South Australia.** 25 miles west-northwest of Welbourn Hill Homestead, *Eichler 17242* (AD). **Northern Territory.** 29 miles east of Curtin Springs H.S., *George 5007* (PERTH). **Western Australia.** Gunbarrel Hwy., 22 miles west of Browne Range, *George 5405* (PERTH); 4 miles east of Mt. Beadell,

George 5388 (PERTH); near Giles Creek, *George 4943* (PERTH); 10 miles northeast of old Minnie Creek H.S., *George 4659* (PERTH); 6 miles west of Mt. Morgans, *George 4127* (PERTH); 14 miles north of Mt. Magnet, *George 762* (PERTH); Glenorn Station, *Burbidge 274* (PERTH).

Microlepidium F. Mueller, Linnaea 25:371 1853.

Plants small glabrous or pubescent annuals, stems erect or spreading; basal leaves entire or remotely dentate, rather fleshy; cauline leaves similar but smaller; sepals spreading and often persistent, rarely saccate; petals creamy and broadly obovate or absent; ovules 2–9 in each locule; siliques round to cuneate, emarginate, partially or entirely winged, the seminiferous part terete or slightly obcompressed; styles short or obsolete; seeds ellipsoid, not flattened, the testa mucos when moistened; cotyledons incumbent. Type species: *Microlepidium pilosulum* F. Muell.

EXCLUDED SPECIES: *Microlepidium fenestratum* F. Muell. ex Ruprecht=*Hymenolobus procumbens* (L.) Nutt. ex Schinz & Thellung.

KEY TO THE SPECIES OF MICROLEPIDIUM

Plants pubescent, often much branched; petals broadly obovate, about 1 mm. long; siliques cordate or cuneate, winged in the distal third. . . . . 1. *M. pilosulum.*
Plants glabrous, the stems usually simple; flowers apetalous; siliques round to cordate, winged the entire length. . . . . 2. *M. alatum.*

1. Microlepidium pilosulum F. Muell.

MAP 3

Microlepidium pilosulum F. Muell., Linnaea 25:371. 1853. Lectotype: South Australia. Murray scrub, *F. Mueller* (MEL *10927*).

Capsella pilosula (F. Muell.) F. Muell., Plants Indig. Colony Victoria 1:44. 1862.

Plants erect or spreading annuals, pubescent; trichomes simple or bifurcate, the simple ones often flattened; stems to 2 dm. long, decumbent and often much branched and intertwined; basal leaves to 2 cm. long, obovate, entire or remotely dentate, withering early and usually lost; cauline leaves to 1.5 cm. long, narrowly obovate, entire or coarsely dentate toward the distal end; inflorescences initially dense and fasciculate, elongating after anthesis, buds subglobose; sepals 0.8–1.5 mm. long, elliptic or obovate, not saccate, but often cucullate and the lateral sepals often distally lobed; petals 0.7–1 mm. long, roughly obovate with a sub-orbicular blade narrowed to a short broad claw, emarginate or trilobed distally; stamens 0.7–0.9 mm. long, the filaments enlarged at the base; glandular tissue fleshy, conical on each side of each single stamen, between the paired stamens absent or barely developed; ovules 2–9 in each locule; infructescences loose, the pedicels to 4 cm. long, usually less than 2 cm., stout and rigid, spreading horizontally from the stem; siliques 3–4.5 mm. long, cordate or cuneate with a broad shallow notch, slightly obcompressed, the valves glabrous on the interior, on the exterior glabrous or sparsely pubescent with short simple trichomes, winged in the distal third; styles very short or obsolete; stigmas depressed-capitate or obscurely bilobed; septum often fenestrate; seeds 0.6–0.9 mm. long, ellipsoid and plump, orange or orange-brown.

DISTRIBUTION: Western Australia, South Australia, including Kangaroo Island, and western Victoria.

OTHER SPECIMENS SEEN: **Victoria.** Lower Glenelg River, *Eckert* 52 (MEL *10941*); Yambuk, *Williamson* (MEL *10929*); Port Fairy, *Williamson* (BM,MEL *10937, 10938,*

10939, 10940); coast, hills near Goose Lagoon—Port Fairy, *Willis*, 1947 (MEL *10930*). **South Australia** (mainland). Colona Homestead, *Willis*, 1947 (MEL *10930*); between Eucla and Fowler's Bay, *Richards*, 1883 (MEL *10931*); Fowler's Bay, *Richards*, 1879 (AD); Fowler's Bay, about 6 km west along roadside, *Whibley 611* (AD); Minnipa, *Dept. Agric. 499* (AD); Davenport Creek, Eyre Peninsula, *Cleland*, 1928 (AD); Yorke Peninsula, *Tepper* (MEL *10932, 10933, 11017*); Morgan, *Tate*, 1882 (AD); ad fl. Murray ostium versus, *F. Mueller* (MEL *10926*); mouth of Murray River, *F. Mueller* (K). **Kangaroo Island.** On sandhills about 3¾ km. southwest of Kelly Hill, *Eichler 15206* (AD); Flinders Chase, West Bay, 16 km. south of Cape Borda, *Wilson 948* (AD); sandhill on road to Cape de Couedic, 1½ km. south of Rocky River Homestead, *Eichler 15379* (AD). **Western Australia.** Israelite Bay, *Brooke*, 1885 (MEL *10936*).

The plants sometimes are elaborately branched and entangled with others as in Whibley's collection (611) made near Fowler's Bay; the original collection included both *Microlepidium pilosulum* and *M. alatum*. The inflorescences are very short and dense as in *Lepidium fasciculatum* and elongate only after fruit development is well-advanced. Often the secondary stems are reduced to a single flower which then arises in the axil of a sessile upper cauline leaf so the inflorescence appears to be bracteate.

Microlepidium pilosulum is one of the very few species of Cruciferae known from Kangaroo Island where it seems to be restricted to Flinders Chase at the western end of the island. The known distribution is predominantly coastal except for isolated collections made at Minnipa on the Eyre Peninsula and at Morgan. This species might be looked for in the upper southeast of South Australia and along the southeastern coast.

2.**Microlepidium alatum** (J. M. Black) E. Shaw, comb. nov.

Hymenolobus alatus J. M. Black, Trans. Roy. Soc. S. Austral. 67:36. 1943. Holotype: South Australia. "In shady spots near Wudinna Eyre Peninsula," *C. W. Johns* (AD), probable isyotpes (AD).

Plants small spreading or erect annuals, glabrous; stems to 2 dm. long, stout and rigid, rarely branched; basal leaves to 2 cm. long, the blade obovate and usually entire, narrowed into a slender petiole; cauline leaves to 1.5 cm. long, scattered and few, obovate and entire or remotely dentate, the upper ones sessile; inflorescences elongating after anthesis, the buds globose; sepals 1–2 mm. long, (ob-)ovate or elliptic, rarely saccate but often cucullate; petals none; glandular tissue square around the single stamens, absent between the paired stamens; ovules 4(5) in each locule; infructescences loose and elongate, the pedicels 2–3.5 cm. long, erect to spreading, often horizontally so; siliques 4–5.5 mm. long, round to cordate with a deep distal notch and broadly winged, the seminiferous part of the fruit terete or slightly obcompressed, the valves alate their full length with a flat solid wing; styles very short or obsolete, the stigmas depressed-capitate; septum entire; seeds 0.8–1 mm. long, broadly ellipsoid, dull orange or orange-brown.

DISTRIBUTION: South Australia. Known only from Wudinna in the upper Eyre Peninsula and from Fowler's Bay on the Bight.

OTHER SPECIMENS SEEN: **South Australia.** Wudinna, *Ising* (AD), *C. W. Johns* (AD); Fowler's Bay, about 6 km. west along roadside, *Whibley 611* (AD).

Although Black described this species as pubescent with appressed trichomes, I have seen only glabrous plants. The stems are angular with a row of membranous, semi-elliptic wings on each angle and Black may have thought these to be trichomes. He also described the flowers as having four stamens—only the paired ones developed—but the full complement of six usually is present. The inflorescences, which initially are dense as in *Microlepidium pilosulum*, elongate at anthesis, and the infructescences, which may take up nearly the entire length of the stem, are very long in proportion to the size of the plant.

Ballantinia E. Shaw, gen. nov.

Plantae annuae, pubescentes trichomatibus simplicibus vel irregulariter ramosis; folia (basalia et caulina) plerumque pinnatim lobata; petala unguiculata, sepalis duplo longiora; ovulae 2–6 in loculo; siliquae in receptaculo sessilies, ellipsoideae vel late obovoideae et parum compressae, ad apicem acutae; styli brevissimi vel nulli; stigmata capitata; semina ellipsoidea in statu humefacto mucosa; cotyledones incumbentes. Type species: *Ballantinia antipoda* (F. Muell.) E. Shaw.

For the name *Ballantinia* I am indebted to J. D. Hooker who annotated the holotype sheet of *Hutchinsia australis* Hook. f. as "Ballantinia Hutchinsinioides," a name which never was published. Miss Mary Ballantine (or Ballantyne) supplied to Ronald Gunn, who forwarded them to Hooker, plants collected along the River Derwent in Tasmania. I include in *Ballantinia* one species found in both central Victoria, whence it was described by Mueller in 1854 as *Capsella antipoda*, and in central Tasmania, described from this state by Hooker in 1860 as *Hutchinsia australis*.

In Schulz's scheme *Ballantinia* falls into the subtribe Arabidopsidineae of the Sisymbrieae, including genera characterized by fruit which are dehiscent, round in section or compressed, but never obcompressed, leaves not amplexicaul, embryos notorhizal, calyx spreading, filaments sometimes expanded at the base, anthers obtuse and the seeds mucose. Schulz's Arabidopsidineae is a morphologically and geographically rather heterogeneous group of 15 genera, eight of which are Australian (*Blennodia* of Bentham's Flora Australiensis); four are American, *Sphaerocardamum*, *Halimolobus*, *Pennellia*, and *Lamphrophragma*; two are from central Asia, *Cymatocarpus* and *Christolea*; and one, *Arabidopsis*, is widespread in temperate parts of Eurasia.

Sphaerocardamum has nearly spherical siliques; two of the Australian genera, *Geococcus*, a small geocarpic annual of southern Australia, and the alpine perennial, *Drabastrum*, have comparatively short, but carinate, siliques. Fruits of the other genera in the subtribe are elongated siliques and *Ballantinia* would seem to be an anomalous intruder into the group. Although Schulz included *Ballantinia antipoda*, as *C. australis*, in *Cuphonotus*, it differs from *Cuphonotus* as here treated, in having compressed, rather than obcompressed, siliques, and flowers with sepals and

stamens only weakly spreading and distinctly unguiculate petals. The Tasmanian-Victorian range of *Ballantinia* also sets it apart from other Australian Cruciferae which are, except for the alpine endemic *Drabastrum*, and species of *Rorippa* and *Cardamine*, predominantly eremaean.

Ballantinia antipoda (F. Muell.) E. Shaw, comb. nov.

MAP 3

Capsella antipoda F. Muell., Trans Phil. Soc. Victoria 1:34. 1854. Lectotype: Victoria. In the Black Forest, *F. Mueller* (MEL *18237*), isolectotype (K).

Cuphonotus antipodus (F. Muell.) J. M. Black, Trans. Roy. Soc. S. Austral. 61:244. 1937.

Hutchinsia australis Hook. f., Flora Tasmaniae 1:23, tab. IV. 1860. Holotype: Tasmania. Macquarie Plains, *M. Ballantine*, 1842 (K), photo (GH). This is the collection cited in the prologue as *Gunn 644;* the plants were collected by Ms. Ballantine near New Norfolk on the Derwent and forwarded by Gunn to Hooker.

FIG. 1. Ballantinia antipoda. Habit (×1½); silique (×8). From plants in *Gunn 644* (K).

Capsella australis (Hook. f.) Bentham, Flora Austral. 1: 81. 1863.
Cuphonotus australis (Hook. f.) O. E. Schulz, Bot. Jahrb. 66:92. 1933.

Perhaps to be included here is *Draba pumilio* R. Br. ex DC., Syst. nat. 2:353. 1821; Prodr. 1:171. 1824. Holotype: Tasmania. Hab. in terra van Diemen, *R. Brown* (G–DC).

Plants prostrate or decumbent annuals, sparsely pubescent with simple or forked acicular trichomes; basal leaves to 2 cm. long, usually deeply pinnatisect, or entire to remotely dentate, the blade then oblong or spathulate and narrowed to a slender petiole; cauline leaves similar but smaller; inflorescences elongating after anthesis; sepals 0.8–1 mm. long, round or broadly elliptic, cucullate but rarely saccate; petals 1.3–2 mm. long, white, distinctly unguiculate, the blade round to deltate and abruptly narrowed to the claw; stamens about 1 mm. long; glandular tissue conical on each side of each single stamen, absent between the paired stamens; ovules 2–6 in each locule; infructescences loose, fruiting pedicels 5–10 mm. long, erect or divaricately spreading; siliques 3–5 mm. long, ellipsoid or broadly obovoid and slightly compressed; styles very short or obsolete, stigmas capitate and flattened; septum entire; seeds about 1 mm. long, ellipsoid and flattened, the testa orange.

DISTRIBUTION: Central Tasmania and in Victoria to the west and northwest of Melbourne.

OTHER SPECIMENS SEEN: **Tasmania.** Banks of Derwent near Glen Leith, *J. D. Hooker 1024* (K); top of Native Tier, Glen Leith, *J. D. Hooker 1023* (K); dry stony places, Tasmania, *J. D. Hooker 1027* (K). **Victoria.** Near Mt. Macedon, *anon.* (MEL *19230*); Werribee, *Fullager* (MEL *18228*); plains near Carsibrook, *anon.* (MEL *18236*); Daylesford, *Wallace,* 1880 (MEL *18232*); Upper Loddon River, *Dickinson,* 1887 (MEL *18229*); Skipton, *Whan* (MEL *18233, 18235*), *Greeves* (MEL *18234*); western part of Victoria, *anon.* (MEL *18227*); western districts of Victoria, *anon.* (MEL *18231*); top of Mt. Alexander, *F. Mueller* (K,MEL *18237*).

The description and citations are based only on material in K and MEL; the range in Tasmania probably can be extended by specimens at HO which I have not seen. As is true of several species of Australian Cruciferae, there are no recent collections of *Ballantinia antipoda*. The figure (tab. IV) in Flora Tasmaniae is good although the petals usually are more sharply unguiculate than shown there. Whatever the differences between the Victorian and Tasmanian populations might be, they are minute. The few specimens from Tasmania which I have seen have shorter styles and a greater proportion of simple trichomes than do those from Victoria.

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REVISION OF THE GENUS MOSCHARIA (COMPOSITAE: MUTISIEAE) AND A REINTERPRETATION OF ITS INFLORESCENCE

JORGE VÍCTOR CRISCI[1]

Moscharia is a small genus of annual herbs in the tribe Mutisieae subtribe Nassauviinae. This genus is restricted to central Chile, and occurs from Coquimbo to Maule. It is found from sea level to an altitude of ca. 2,000 meters. This paper presents the description of a new species of this hitherto monotypic genus and a new interpretation of the unique floral head of *Moscharia*.

ACKNOWLEDGEMENTS

The present study was completed at the Gray Herbarium of Harvard University during my tenure as a Fellow of the John Simon Guggenheim Memorial Foundation. I I am grateful to the officers of both these institutions for their support of my work. I also appreciate the guidance of Dr. Otto T. Solbrig and the help and advice of G. L. Stebbins, Jr., E. A. Shaw, T. F. Stuessy, S. Carlquist, A. L. Cabrera. K. S. Bawa, V. M. Toledo, R. C. Rollins, K. Roby, C. E. Wood, Jr., Arthur Cronquist, Otto Zöllner, and especially the constant help of my wife Marta, who also prepared the illustrations.

The abbreviations for herbaria listed in the citation of specimens are taken from the fifth edition of the Index Herbariorum (Lanjouw and Stafleu, 1964).

THE PROBLEM OF THE CAPITULUM OF MOSCHARIA

In the Compositae one often observes a reduction of the number of flowers in the capitula and the aggregation of the capitula themselves into a capitate secondary inflorescence (pseudocephalium of Troll, 1928). Approximately 70 genera (7% of the genera in the family) have pseudocephalia, and are distributed in 11 of the 12 tribes of the subfamily Asteroideae. However, they are absent from the subfamily Cichoroideae. A third order of aggregation, a capitulum composed of pseudocephalia, is found in the genus *Triphocephalium* in the tribe Inuleae.

The presence of pseudocephalia is believed to be an advanced evolutionary feature compared to a regular capitulum. Stebbins (1967) has suggested that pseudocephalia result from selection for an increase in the total number of flowers in a secondary inflorescence and that such selection operates on species in which the number of flowers in a capitulum were previously reduced in response to a different kind of selection. According to Stebbins, the union of few-flowered capitula into a secondary head-like inflorescence would be a more efficient mechanism to increase the size of the functional inflorescence than the acquisition of new flowers into a reduced capitulum. If this hypothesis is correct, then the formation of the pseudocephalium is as follows: first, groups of small capitula aggregate closely without loss of their individual identity. Second, these capitula aggregate into a functional head and at this stage the individual capitula are still recognizable and no pseudoinvolucre has

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been formed. The last step is the acquisition of a pseudoinvolucre and the obliteration of the identity of the individual capitula.

Up to the present time, the floral head of *Moscharia* has been considered to be a true capitulum. However, a numerical-morphological study of the genera of the subtribe Nassauviinae (Crisci, in preparation) indicates that the genera *Nassauvia* Juss., *Triptilion* Ruiz et Pavón and *Polyachyrus* Lagasca are all closely related to *Moscharia*. The presence of pseudocephalia in the former three genera led me to investigate *Moscharia* to see if the same inflorescence type was present. Since this study also indicates that *Polyachyrus* is the most closely related genus to *Moscharia*, it is evident that the interpretation of the floral head of *Moscharia* must be based on a comparison of the functional floral heads of these two genera. *Polyachyrus* is a genus of seven or eight species from central and northern Chile and southern Peru; it has two- (rarely three-) flowered capitula aggregated into oval, very compact pseudocephalia, with each capitulum growing in the axil of an accessory bract. These pseudocephalia correspond to the second step of the evolutionary series described above, since they have no pseudoinvolucre. The primary capitula are small and have an involucre of five bracts, the outermost of which is larger than the others. It is keeled and has a fleshy hump on the dorsal surface. The keeled bracts envelop one of the two flowers as well as one of the other bracts; the other three bracts surround the second flower. The fifth bract (which also can be interpreted as a palea) is found between the two flowers, and, as mentioned above, is surrounded by the keeled bract (Fig. 1).

Moscharia pinnatifida, the only known species of the genus until now, has been interpreted as having a simple head surrounded by an involucre of 5–8 oval foliaceous bracts. Next on the convex receptacle are found 7–9 bracts arranged in one exterior series. Each of these bracts is keeled and has a hump on the dorsal surface; each bract surrounds two flowers which in turn are separated by a linear bract. Finally, at the center of this series of bract-flower complexes are found 4–7 lanceolate bracts that surround one to two (rarely 1–5) central flowers. No such arrangement of bracts and flowers is known among first order capitula.

If we compare the pseudocephalium of *Polyachyrus* with the floral head of *Moscharia* the real homology of the latter is easy to ascertain. In effect, each group of two flowers and their surrounding bract in the head of *Moscharia* is equivalent to a primary head in the pseudocephalium of *Polyachyrus*, the difference being that the bracts have been reduced from five to two. The central group of one to two flowers and their surrounding bracts correspond to a much reduced first-order head (these bracts probably are comparable with the accessory bracts of the capitulum of *Polyachyrus*). The "capitulum" of *Moscharia pinnatifida* would thus correspond to the last stage in the evolution of a pseudocephalium.

This new interpretation of the floral head of *Moscharia* was confirmed

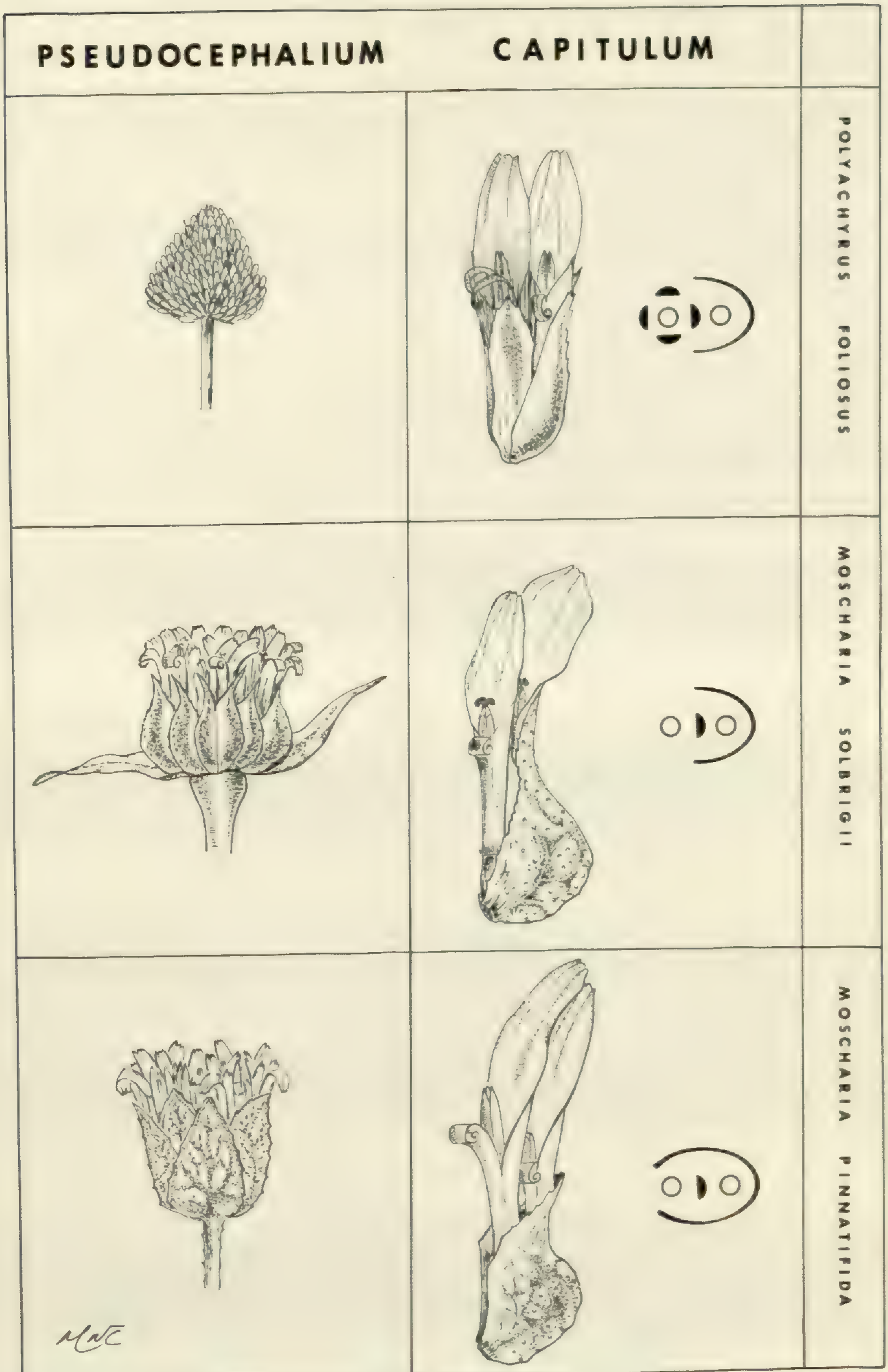


FIGURE 1. Hypothetical sequence of the evolution of the *Moscharia pinnatifida* pseudocephalium from the *Polyachyrus* type of pseudocephalium through *Moscharia solbrigii*. The schematic diagrams represent the section of the capitulum: circles represent flowers; lines represent bracts.

by the discovery of a second species of the genus intermediate between *Polyachyrus* and *Moscharia pinnatifida*. This species, *Moscharia solbrigii*, has no pseudoinvolucre, the keeled bract has a fleshy hump like that in *Polyachyrus* and this bract envelops only one of the two flowers. Sometimes a reduced third bract, that is the equivalent of one of the three bracts surrounding the inner flower in *Polyachyrus*, is found at the side of the inner flower in *M. solbrigii*.

The great reduction of the capitula of *Moscharia pinnatifida*, their close aggregation, and the presence of a pseudoinvolucre led to the erroneous interpretation of its flower head. Figure 1 compares the pseudocephalia and capitula of *Polyachyrus foliosus* and the two species of *Moscharia*.

Taxonomic History of the Genus

Moscharia was described by Ruiz and Pavón in 1794, in a paper that contained descriptions of plants from Peru and Chile. No specific name and no localities were given in the original description. *Moscharia* Ruiz and Pavón is a *nomen conservandum*. Conservation was necessary because it is a later homonym of *Moscharia* P. Forskål (Floral Aegyptiaco-Arabica 158. 1775) which is considered to be a synonym of *Ajuga* L. (Labiatae).

Ruiz and Pavón described the first species of *Moscharia (M. pinnatifida)* in 1798. The localities were "in Regni Chilensis aridis, arenosis et petrosis locis ad Aconcaguae, Quillotae et Rancaguae Provincias et copiose versus S. Jacobi Chilensis urbem." In 1807 Persoon, without any explanation, made an orthographic variant for *Moscharia* Ruiz and Pavón: *Moscaria*. (It is possible that this could be only a typographical error). In 1810, Molina took notice of the existence of the name of Forskål, and changed the name of the genus of Ruiz and Pavon to *Moschifera*. Then in 1826 Sprengel, without any explanation, gave a new name, *Mosigia*, for this genus. At the same time he put the taxon in the tribe Cichoreae (Lactuceae). Between 1827 and 1829 David Don described a new genus from Chile, *Gastrocarpha*, with only one species *(G. runcinata)*. Lessing (1832) showed it to be synonymous with *Moscharia*.

SYSTEMATIC TREATMENT

Moscharia Ruiz et Pavón

Moscharia Ruiz et Pavón, Prodromus Flora Peruvianae et Chilensis 91. 1794, nom. cons. (non Moscharia Forskål, Flora Aegyptiaco-Arabica 158. 1775, *Labiatae*).

Moscaria Persoon, Synopsis Plantarum 2:379. 1807.

Moschifera Molina, Saggio 2:294. 1810.

Mosigia Sprengel, Systema Vegetabilium 3:366. 1828.

Gastrocarpha Don, in Sweet, British Flower Garden 3: t. 229. 1827–1829.

Herbaceous annuals, pubescent with four kinds of trichomes: glandular, uniseriate, 3–9 celled, 70–160 μ long, borne on leaves, stems, bracts, corolla and sparsely on the achenes; non-glandular, uniseriate, few celled, 50–70 μ long, borne on the pseudoinvolucre and corolla; double trichomes of 2 cells (Zwillingshaare of Hess) 40–60 μ long, joined along their inner wall, present on the achenes; and one-celled trichomes,

60–112 μ long, on bracts and corolla. Stems erect, terete in cross section, branched toward the apex. Leaves simple, alternate, apex acute; stem leaves sessile, amplexicaul, entire or lobed; basal leaves and sometimes the first 5 or 6 stem leaves elliptic, petiolate, pinnately parted. Petiole vaginate, compressed at the base. Inflorescence terminal, pseudocephalium in a many-branched cyme. Pseudocephalium with 8–10 capitula, with or without a uniseriate pseudoinvolucre of 5–8 ovate, membranaceous, foliaceous bracts. Capitula sessile, of two kinds, 7–9 outer ones and a single central one. Outer capitula 7–9 in a single series around the margin of the pseudocephalium, each capitulum with two flowers, the involucre reduced to two bracts, the outer one both keeled and with a sometimes fleshy hump conduplicate around either the outer flower and the second (inner) bract or around both these and the inner flower; inner bract (palea?) between the two flowers linear-lanceolate, scarious, bi- or tridentate at the apex, flowers hermaphroditic, the outer flower with a pappus, the inner flower with or without a pappus. Central capitulum of the pseudocephalium with 1 or 2 flowers (rarely 1–5) and a uniseriate involucre, composed of 4–7 lanceolate, scarious bracts; flowers hermaphroditic, with or without a pappus. Receptacle of the pseudocephalium convex, glabrous. Corolla bilabiate, pubescent, the tube broader toward the apex; outer lip lanceolate, liguliform, with four veins, the apex three-toothed; inner lip bifid. Stamens five, the filament inserted at a point halfway from the base of the tube; anthers connate, each with an oblong apical appendage and a tailed base. Style bifid, its branches flattened, truncate, with a crown of elongate collection hairs at the apex and papillose with shorter ones on the adaxial surface, glabrous on the abaxial surface. Achenes fusiform, with double trichomes. Pappus uniseriate of 10–20 short scales. Pollen grains zonocolporate (3), prolate spheroidal; ends of colpi rounded, membrane of colpi smooth; structure of tectum irregular, with a thin layer under the terminal membrane; infratectum baculate; tectum and infratectum separated from each other by a thin layer not parallel to the nexine (zig-zag). Two species in the region of central Chile (Map 1). Type species: *Moscharia pinnatifida* Ruiz et Pavón.

Moscharia is a member of the tribe Mutisieae subtribe Naussauviinae which is characterized by bilabiate corollas with the outer lip three-toothed and the inner lip bifid, anthers long-tailed at the base, and style bifid with branches truncate at the apex. *Moscharia* can be easily distinguished from all the other genera of the subtribe by the presence of pseudocephalia composed of 8–10 capitula, attached at the same level and by outer capitula with the involucre reduced to two bracts, one of them keeled. The greatest affinity of *Moscharia* is with *Polyachyrus*, which also has pseudocephalia but with many more than 10 capitula; the capitula are disposed in the pseudocephalium at different levels. The name of the genus comes from Latin for "musky" because of the strong musky odor of the plants. The common name is "almizclillo" or "almizcle," which in Spanish also means musky.

The two species of *Moscharia* can be easily distinguished as shown below:

Moscharia pinnatifida

Pseudocephalia with pseudoinvolucre

Flowers pale pink

Keeled bract with apex incised, abaxial surface scarcely pubescent, hump not fleshy, bract conduplicate around the two flowers and the inner bract.

Only the outer flower of the outer capitula with a pappus.

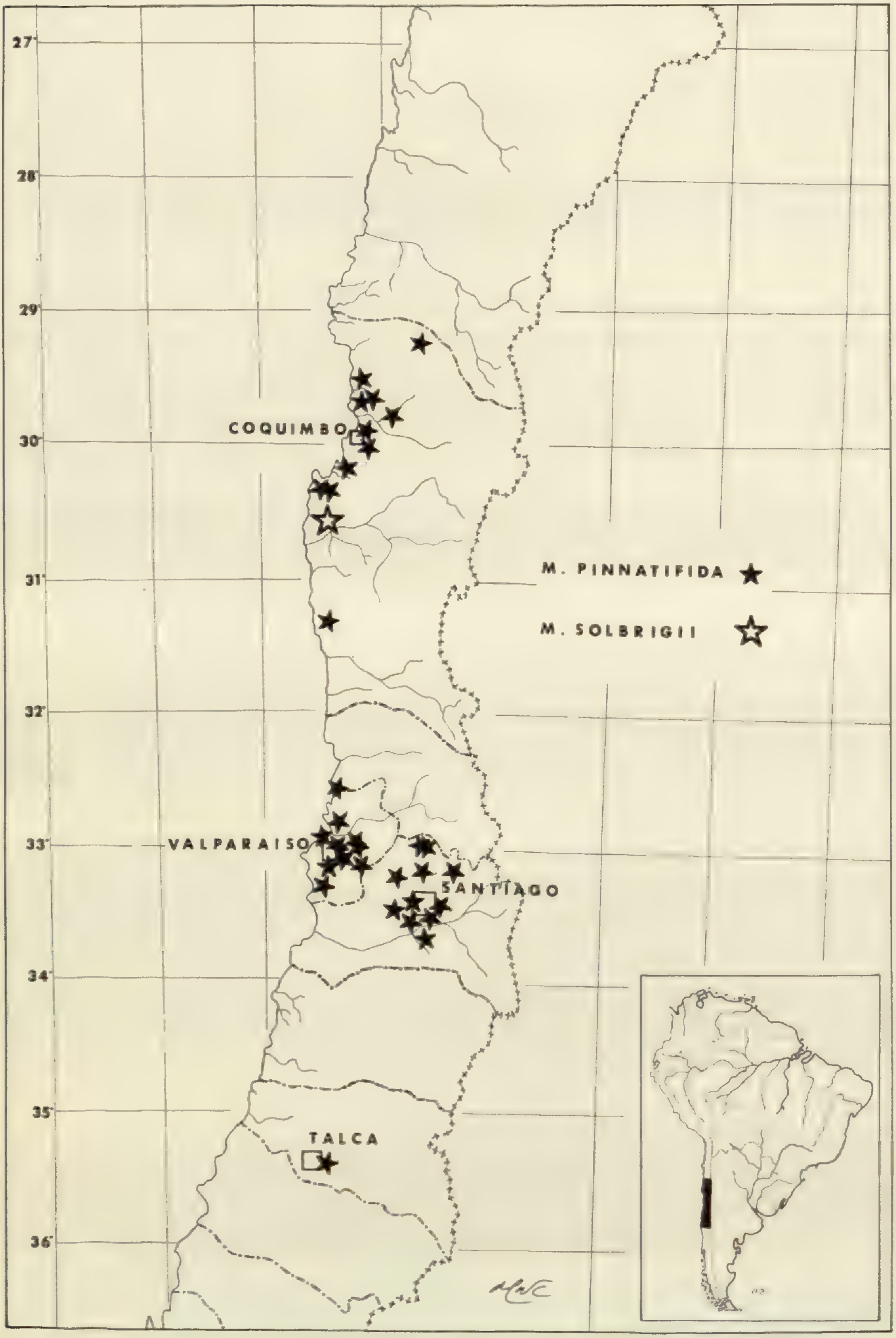
Moscharia solbrigii

Pseudocephalia without pseudoinvolucre

Flowers lavender

Keeled bract with apex acute, abaxial surface densely pubescent, hump fleshy, bract conduplicate around the outer flower and the inner bract, not the inner flower.

All flowers with a pappus.



Map 1. Distribution map of the species of *Moscharia* Ruiz et Pavón.

Moscharia pinnatifida Ruiz et Pavón

Figure 2

Moscharia pinnatifida Ruiz et Pavón, Systema Vegetabilium: 186. 1798.
Moscaria pinnatifida (Ruiz et Pavón) Persoon, Synopsis Plantarum 2:379. 1807.
Moschifera pinnatifida (Ruiz et Pavón) Molina, Saggio 2: 294. 1810.
Mosigia pinnatifida (Ruiz et Pavón) Sprengel, Systema Vegetabilium 3:661. 1826.
Gastrocarpha runcinata D. Don in Sweet, British Flower Garden 3: t. 229. 1827–1829.

Plants annual with a strong odor, 30–70 cm. tall, stem erect, pubescent, much branched toward the apex, with leaves all along it. Basal leaves and the 5 or 6 lowest stem leaves pubescent, petiolate, elliptic, pinnately parted, with dentate segments, 10–18 cm. long, 2–3 cm. wide. Stem leaves sessile, pubescent, amplexicaul, entire or lobed, the uppermost lanceolate. Petiole vaginate, compressed at the base. Capitula in pseudocephalia. Pseudocephalia hemispherical, 5–8 mm. in diameter and 10 mm. high. Pseudoinvolucre of 5–8 foliaceous bracts; bracts acute at the apex, densely pubescent on the adaxial surface, ovate, membranaceous, 6–8 mm. long and 4–6 mm. wide. Outer capitula 7–9, in one series at the margin of the pseudocephalium; outer bract of each capitulum strongly keeled and with a hump, scarcely pubescent on the adaxial surface, conduplicate around the two flowers and the inner bract, incised at the apex, 4–5 mm. high; inner bract scarcely pubescent on the margin, linear-lanceolate, 3.5–4 mm. long and 0.5–0.8 mm. wide, 2 or 3 toothed at the apex; flowers two, hermaphroditic; the inner flower without a pappus. Inner capitulum with an involucre of 4–7 bracts, bracts lanceolate, scarious, 2 or 3 toothed at the apex, 2–2.5 mm. long and 0.3–0.4 mm. wide; flowers 1–5, hermaphroditic, with a pappus. Corolla pale pink, pubescent, 10–11 mm. long; tube 4–6 mm. long, 0.5–0.7 mm in diameter at base and 1–1.1 mm. at apex; outer lip 4–veined, three toothed at apex, 3–5 mm. long and 2–2.5 mm. wide; inner lip bifid, 3–4 mm. long, each lobe 0.5–0.6 mm. wide. Anthers tailed, glabrous, 5-6 mm. long; style bifid, the branches 1.3–1.5 mm. long. Achenes 1–.50 mm. long, 0.3–0.4 mm. in diameter, scarcely pubescent. Pappus of 18–20 scales 1 mm. high, uniseriate, white, present only in outer flowers of outer capitula.

DISTRIBUTION: Central Chile from Coquimbo to Maule, from sea level to almost 2,000 meters altitude; flowering from August to December.

SPECIMENS EXAMINED. **Chile. Provincia de Coquimbo.** Fray Jorge, *Skottsberg 755* (F,NY), *Muñoz 209* (GH); La Serena, Punta de Teatinos, *Wedermann 876* (F,GH,M,NY, (F,NY), *Muñoz 209* (GH); La Serena-Vallenar route, *Morrison 16281* (GH,UC); Coquimbo, *Harvey s.n.*, UC,US); La Serena-Vallenar route, *Morrison 16281* (GH,UC); Coquimbo, *Harvey s.n.*, 1856 (GH), *Jaffuel 2691* (GH); Guayacán, *Cabrera 11386* (F); Quebrada de la Niña, Corral de Julio, *Simon 294* (UC); Los Chorrillos, *Poeppig 237* (NY). **Provincia de Valparaiso.** Valparaiso: *Buchtien*, 1895 (US), *Claude Joseph 3575* (US), *Bertero s.n.* (F,1012113), *Borchers s.n.*, 1883 (F), *Jaffuel 552* (GH), *Behn s.n.*, 1922 (F); Curauma: *Behn s.n.*, 1929 (F,UC); Laguna Verde: *Garaventa 1642* (GH); Quillota: Cerro Caquis, *Morrison 16898* (GH,UC). **Provincia de Aconcagua.** Zapallar: Quebrada del Barraco, *Kausel 2585* (F). **Provincia de Santiago.** Santiago, Cerro San Cristobal: *Skottsberg 981* (F); Santiago: *Philippi s.n.*, 1888 (US), *Claude Joseph 513, 514* (US), *Germain s.n.* (F); (F,NY), *Hastings 80* (NY,UC,US),*Montero 700* (F), *Looser 678, 776* (GH), *Kausel 2475* La Reina: *Frödin 20* (NY); Tiltil: *Montero 151* (F); Montenegro: cordillera de la costa, *Zöllner 6491, 6492* (GH); Renca: *Gigonx s.n.*, 1886 (GH). **Provincia de Talca.** Talca: *Claude Joseph 2053* (US). **Without localities or localities not identified:** *Gay*, 1833 (P); *Bridges s.n.* (GH); *Bunge s.n.* (F, 1012091); *Basil s.n.* (NY); *Basil*, 1838 (NY); *Gillis s.n.* (NY); *Bertero 1404* (NY); 1834 (GH); *Caldcleugh s.n.* (F, ex G syntype of *Gastrocarpha runcinata*?); Rio Claro, *Guillemin s.n.* (GH), *Bertero s.n.*, 1828 (GH); Muñoa, *Claude Joseph 2097* (NY,US).

This species is very widespread and abundant. According to Reiche

FIGURE 2. *Moscharia pinnatifida* Ruiz et Pavón (*Zöllner 6491*, GH). a. Habit, × ⅓; b. Pseudocephalium, × 2: c. Marginal capitulum, × 5; d. Marginal capitulum longitudinal section, × 5; e. Involucral bract of marginal capitulum, × 8; f. Involucre of central capitulum, × 10; g. Flower, pappus and ovary not shown, × 5; h. Achene, × 5; i. Stamen, × 7.5; j. Style arms, × 35.

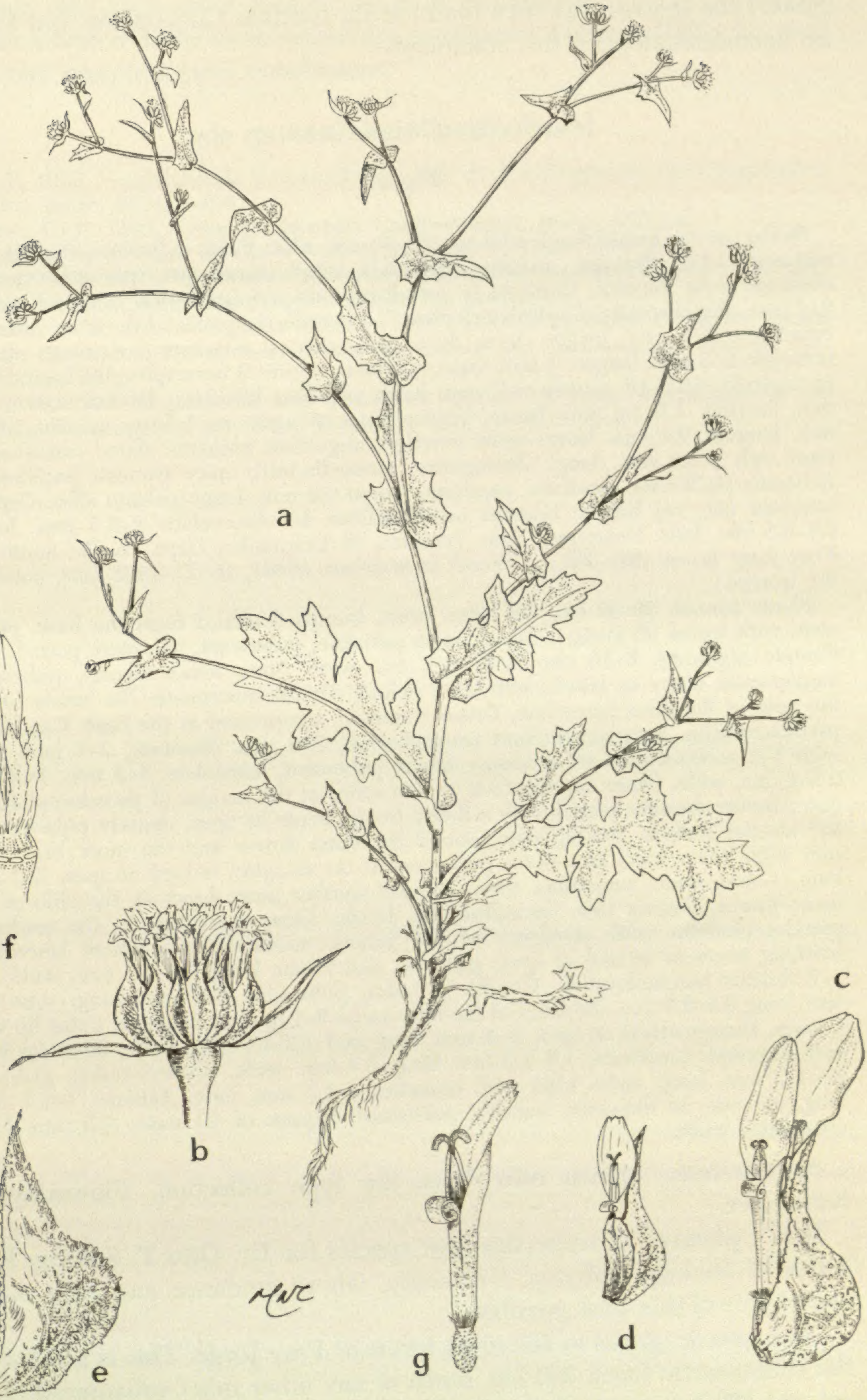


FIGURE 3. *Moscharia solbrigii* Crisci sp. nov. *(Worth & Morrison 16441)*. a. Habit, × ½; b. Pseudocephalium, × 4; c. Marginal capitulum, × 10; d. Marginal capitulum without inner flower, × 5; e. Involucral bract of marginal capitulum, × 12; f. Central capitulum, × 5; g. Flower, × 5.

(1905) the species was once found as far south as Concepción, but I have no documentation for this statement.

Moscharia solbrigii Crisci, sp. nov.

Figure 3

Herba annua hispidulo-glandulosa, 20–30 cm. alta. Folia radicalia petiolata, pinnatisecta lobis dentatis; caulina auriculata amplexicauliaque, pinnatisecta lobis oblongis acute dentatis. Capitula in pseudocapitulis hemisphaericis 5–6 mm. crassis, 3–4 mm. altis disposita. Capitula exteriore 7–8; involucri squamae biseriatae, exteriores cucullatae 3–4 mm. longae dorso dense pubescentes, interiores lanceolate planiusculaeque 2–3 mm. longae, 1 mm. latae, scariosae. Flores 2 hermaphroditi lavandulacei in capitulo exteriore; corolla 6–7 mm. longa papillosa bilabiata; labium exterius 3–4 mm. longum, 1.5–1.6 mm. latum, ligulaeforme tridentatum; labium interius 1.5–1.6 mm. longum, 0.4 mm. latum quam exteriore angustius; antherae alatae caudataeque; rami styli 1–1.2 mm. longi, divergentes, semicylindrati, apice truncati papillosique. Achaenia fusiformia, erostrata, papillosa, pappo 0.5 mm. longo paleato albo. Capitula interiora uni- vel biflora, bracteis involucralibus 4–7 lanceolatis 2–2.5 mm. longis, 0.4–0.5 mm. latis. Holotype: Chile. Provincia de Coquimbo, Dept. Ovalle. South end Fray Jorge forest, 300–500 m., *Worth & Morrison 16441*, 16–XI–1938 (GH, holotype; UC, isotype).

Plants annual, 20–30 cm. tall. Stem erect, branched almost from the base, pubescent, with leaves all along it. Basal leaves petiolate, pubescent, pinnately parted, with dentate segments, 8–10 cm. long, 2–3 cm. wide. Stem leaves sessile, pubescent, amplexicaul, entire or lobed, with lobes oblong dentate-mucronate; the leaves toward the apex of the plant lanceolate. Petiole vaginate, compressed at the base. Capitula in pseudocephalia. Pseudocephalium hemispherical, 5–6 mm. diameter, 3–4 mm. high, with 1–2 accessory bracts; accessory bracts pubescent, lanceolate, 4–5 mm. long and 0.5–1 mm. wide. Outer capitula 7–8, in one series in the margin of pseudocephalium; outer bracts strongly keeled with a fleshy hump, acute at apex, densely pubescent at the abaxial surface, conduplicate around the outer flower and the inner bract, 3–4 mm. high; inner bract lanceolate, pubescent at the margins, incised at apex, 2–3 mm. long, 1 mm. wide, sometimes there appears another inner bract at the side of the inner flower; flowers two, hemaphroditic, fertile. Inner capitulum in the center of pseudocephalium, with involucre of 4–7 bracts, uniseriate; the bracts lanceolate, scarious, acute or incised at apex, glabrous, 2–2.5 mm. long, 0.4–0.5 mm. wide; the 1–2 flowers hermaphroditic. Corolla lavendar, pubescent, 6–7 mm. long; tube 2–3 mm. long, 0.4–0.5 mm. diameter at the base and 0.8–1 mm. at the apex; outer lip with 4 veins, three-toothed at apex, 3–4 mm. long and 1.5–1.6 mm. wide; inner lip bifid with segments connivent, 1.5–1.6 mm. long, 0.4 mm. wide. Anthers tailed, glabrous, 2.5–2.7 mm. long; styles bifid with branches 1–1.2 mm. long. Achenes 1–1.1 mm. long, 0.5 mm. in diameter, scarcely pubescent. Pappus of 10 scales 0.5 mm. long, uniseriate, white.

DISTRIBUTION: known only from the type collection. Flowering in November.

It is a pleasure to name this new species for Dr. Otto T. Solbrig, Professor of Biology, Harvard University, whose guidance and help made completion of this work possible.

This species grows in the relict forest of Fray Jorge. This is a relict of the subantarctic forest 250 km. north of any other relict subantarctic forest and 500 km. north of the northern border of that type of vegetation. Since the subantarctic forest is presumed to have been shifted northward during the Pleistocene (Solbrig, 1973), it is very likely that *Moscharia*

solbrigii may be a relict species, while *M. pinnatifida* may be a derived species adapted to the more recent dry conditions. This possibility fits well with our morphological conclusions.

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